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POST-FIRE REGENERATION OF WHITEBARK PINE: PATTERNS OF SEEDLING ESTABLISHMENT AND NUTCRACKER SEED DISPERSAL ACTIVITY

BY
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FINAL REPORT for RESEARCH COOPERATIVE AGREEMENT with UNIVERSITY OF COLORADO AT DENVER #INT-87218

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FINAL REPORT

POST-FIRE REGENERATION OF WHITEBARK PINE: PATTERNS OF SEEDLING ESTABLISHMENT AND NUTCRACKER SEED DISPERSAL ACTIVITY

from

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PREFACE

The Final Report for the cooperative project, "Post-fire regeneration of whitebark pine: patterns of seedling establishment and nutcracker seed dispersal activity", is composed of two draft manuscripts that will be submitted to a technical journal in the field of ecology after further revision and review. Between the two manuscripts, the important data collected during the project and the conclusions reached are thoroughly covered .

The inclusive dates of the study were Feb. 2, 1987 to June 1, 1989. The original objectives of the study, as outlined in the Draft Study Plan of June, 1987, were as follows:

1) Determination of patterns of whitebark pine, P. albicaulis, post-fire regeneration with respect to:
   a. distance of seedlings from potential seed source
   b. density of seedlings vs. distance from nearest edge of the burn.
   c. age of seedlings vs. distance from nearest edge of burn
   d. seedling site characteristics

2) Determination of patterns of Clark's nutcracker seed dispersal behavior with respect to:
   a. distances traveled by birds from edge of burn into burned area for seed caching activities
   b. occurrence of cone-bearing whitebark pine trees in vicinity of burn perimeter
   c. nutcracker seed harvesting activities in trees adjacent to burn and preferred caching areas

The study areas were the Sleeping Child Burn and The Saddle Mountain Burn in the Bitterroot National Forest. All the objectives under #1 have been realized. Whitebark pine regeneration patterns appear to follow a negative exponential distribution. The linear model derived from the regeneration curves may be generally applicable, an unexpected benefit of the study.

Only objectives a and b under #2 were completed. Because there were no whitebark pine cones produced in both summers of the study, nutcrackers could not be observed harvesting and caching seeds. I hope to follow up this work with observations of seed harvesting and caching by nutcrackers in the study areas when there are cone crops.

Overall, the Cooperative project was successful and, I believe, made a useful contribution to our knowledge of the ecology of whitebark pine. The experience was greatly enhanced by the opportunities to talk with Fire Sciences Laboratory researchers and their logistical support.

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POST-FIRE REGENERATION PATTERNS OF A BIRD-DISPERSED PINE, *PINUS ALBICAULIS*[1]

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Running head: *Pinus albicaulis* regeneration patterns

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Abstract. The large, wingless seeds of Pinus albicaulis are dispersed primarily by Clark's Nutcracker (Nucifraga columbiana). Periodic fires followed by seed dispersal renew seral P. albicaulis communities in the northern Rocky Mountains. We studied P. albicaulis regeneration in the Sleeping Child and Saddle Mountain Burns of western Montana, predicting 1) regeneration patterns different from those of forest associates and 2) an advantage to P. albicaulis over its competitor A. lasiocarpa under circumstances unfavorable to seed dispersal by wind.

At nearly half of the P. albicaulis sites in both burns, regeneration was in clusters of 2 to 10 seedlings or trees. Plots of regeneration density vs. distance from the seed source produced negative exponential curves and similar linear models in both burns for P. albicaulis; density vs. distance curves differed for the other conifers. Data suggested that seed dispersal by nutcrackers results in higher densities of P. albicaulis relative to A. lasiocarpa early in succession, when the burned area is very large and prevailing winds are against the direction of the burn.

Key words: Abies lasiocarpa; Clark's nutcracker; fire; forest regeneration; Nucifraga columbiana; Picea engelmannii; Pinus albicaulis; Pinus contorta; Pseudotsuga menziesii; seed dispersal; whitebark pine.

INTRODUCTION

In the northern Rocky Mountains, Pinus albicaulis (whitebark pine) forms climax communities on dry subalpine sites and at timberline elevations. Throughout most of the subalpine zone, however, the species is a pioneer that is replaced by shade-tolerant conifers (Arno 1986, Arno and Hoff 1989). Historically, seral P. albicaulis communities were renewed by fire at intervals of 50 to 300 years (Arno 1980, Romme 1980, Arno and Petersen 1983), but the fire suppression practices of the last 80 years have resulted in advanced succession throughout much of the northern Rocky Mountains. This, in conjunction with mountain pine beetle (Dendroctonus ponderosae) epidemics in mature P. albicaulis stands and infection by introduced white pine blister rust (Cronartium ribicola), which kills young trees and reduces seed production in older trees, has resulted in declining populations, senescence of trees, and, consequently, severely reduced seed sources (Arno 1986, Kendall and Arno 1989).

The decline of P. albicaulis is particularly unfortunate because of the value of its seeds as a wildlife food source and its intrinsic ecological interest. Not only do a number of bird and small mammal species feed on the large seeds (Tomback 1978, Smith and Balda 1979, Hutchins and Lanner 1982), but black bears (Ursus americanus) and grizzly bears (Ursus arctos) fatten on the seeds before hibernation (Kendall 1983). In addition, P. albicaulis is the only North American pine of the subsection Cembrae, a taxon with all species dependent on nutcrackers (Nucifraga) - seed-storing corvids - for seed dispersal (Turcek and Kelso 1968, Lanner 1980, Tomback 1983). The seeds of P. albicaulis are dispersed primarily by Clark's

nutcracker (N. columbiana) (Tomback 1978, Tomback 1982, Hutchins and Lanner 1982). Clark's Nutcrackers bury caches of 1 to 15 seeds (or more) under 1 to 3 cm of soil at distances of a few meters to 22 km from parent trees (Vander Wall and Balda 1977, Tomback 1978, Hutchins and Lanner 1982, Tomback 1983). Because P. albicaulis seeds are dispersed by birds, both its seed shadow and population structure differ from that of wind-dispersed conifers (Furnier et al. 1987, Tomback et al. 1989).

We investigated the post-fire regeneration patterns of P. albicaulis in two burns in western Montana, the Sleeping Child Burn and the Saddle Mountain Burn. The pre-fire forests in both areas were seral P. albicaulis communities of the Abies lasiocarpa/Luzula hitchcockii, Vaccinium scoparium phase, habitat type (Pfister et al. 1983), i.e., A. lasiocarpa was the climax species. 1) We predicted that patterns of regeneration differ between P. albicaulis and conifer associates. With the data obtained from the Sleeping Child Burn, we developed a model for the relationship between P. albicaulis regeneration density and distance from a seed wall. This model was tested with data gathered in the Saddle Mountain Burn. 2) With respect to A. lasiocarpa, the most important competitor of P. albicaulis in this habitat type, we asked whether seed dispersal by birds always gives P. albicaulis an advantage in the early seral stages. A companion study (Sund 1988, Sund et al. MS) focuses on the autecology of P. albicaulis in the Sleeping Child Burn, examining regeneration in detail.

METHODS

Study areas

The Sleeping Child and Saddle Mountain Burns are in Bitterroot National Forest, Ravalli Co., west-central Montana. In this region, the primary P. albicaulis elevational range is 2290 to 2620 m (Pfister et al. 1977, Arno and Hoff 1989). P. albicaulis islands occur on exposed or rocky sites at elevations of 2130 to 2290 m. The prevailing winds in late summer and fall are from the northwest, west, and southwest (Finklin 1983, A. I. Finklin, pers. commun, U. S. Forest Service Data: Beaverhead National Forest). The two study areas were selected for similarities in time elapsed since fire, severity of fire, and topography.

The Sleeping Child Burn resulted from an uncontrollable lightning-strike fire in 1961 that consumed about 11,350 ha of forest on the west slope of the Sapphire Range. At the time of the fire, Pinus contorta dominated the lower subalpine (Lotan 1976, Lyon and Stickney 1976). The primary P. albicaulis seed source for the burn is mature forest above 2250 m on the northeastern edge (Fig. 1). Abies lasiocarpa, Picea engelmannii, and P. contorta also occur in this forest. Additional seed sources for these three conifers occur on the other perimeters of the burn and on isolated, small stands within the burn.

The principal study area in the burn is an east-west ridge (i.e., ridge study area) that is 3.7 km long. The east end of the ridge is contiguous with the seed source, and the west end extends into the northern center of the burn (Fig. 1). Elevation along the ridge decreases from about 2480 m to 2170 m with increasing distance from the eastern edge of the burn. A second study area followed a portion

classes were aged. For plots near the Sleeping Child Burn, increment cores were taken about 10 cm above ground level to obtain total ages; for plots near the Saddle Mountain Burn, trees were cored at 1.4 m and the ages adjusted by determined values. Trees less than about 7.5 cm dbh were cut at the base and aged. All ages were obtained by counting rings with a hand lens on exposed trunks or cores.

Plots in burns

At the Sleeping Child Burn, data were collected from 3 to 26 August 1987. Plots were established every 150 m along the ridge study area, following a 3.65 km east-west transect beginning 50 m from the unburned forest at the eastern edge. For each ridge plot established, a parallel plot on the north and south aspect was also established to determine the influence of aspect; but, in a few cases, no representative habitat was available. A total of 63 plots were studied: 21 north, 19 south, and 23 ridge. Details on the effects of aspect are in Sund (1988), Sund et al. (MS.). For the purposes of this study, the data are combined for all plots.

The plot sizes ranged in set increments, with the long axis oriented east-west, from 50 x 1.25 m to 50 x 12 m with respect to local densities of P. albicaulis. For purposes of rapid sampling in areas of high densities, belt widths were smaller, and in areas of low densities, zero densties were avoided by expanding belts. Where P. albicaulis was rare, nested quadrats were used to sample other conifer species.

The road study area was treated as a north-south transect with 14 plots, ranging from 30 x 1.5 m to 30 x 10 m, established on suitable

north aspect sites. The plots ranged in aerial distance to the P. albicaulis seed source from 0.9 to 8.0 km (Fig. 1). Inter-plot road distances ranged from to 0.640 to 2.57 km (for additional details, see Sund 1988, Sund et al. MS.).

Tree regeneration was studied in the Saddle Mounain Burn from 1 to 9 August 1988. Two parallel transects A and B, 10 m apart, began at the steep, southwestern edge of the burn and continued 3.2 km northeast (Fig. 2) Plots were consistently established on the north side of transect A and on the south side of transect B. On the steep, southwestern end of the burn, plots were established every 100 m along each transect for a total of 16. Because of fluctuations in elevation, we increased the number of plots on the northeastern two-thirds of the burn by establishing plots every 50 m along transect A for a total of 15 plots and every 100 m along B for 10 plots. There are discontinuities in transect lines (Fig. 2) because of dense stands of shrubs or bogs. We changed the transect heading at A_{15} and B_{14} to avoid a steep, east-facing slope and to maintain elevations around 2100 m. All 41 plots were 50 m long, with the long axis running from southwest to northeast. Again, set belt widths were used, but as wide as 20 m, with nested quadrats for different species. However, for the first 16 plots and plots B_9 to B18. the sampling area was identical for P. albicaulis and A. lasiocarpa for statistical comparison. The other conifers were not sampled on plots B_9 to B_{16}.

For both burns, plot measurements included elevation and aspect. Aerial distances from the P. albicaulis seed wall to plots were obtained from U.S.G.S. 7.5 minute series topographic maps, the Kent Peak and Jennings Camp Creek Quadrangles for the Sleeping Child Burn

and the Lost Trail Pass Quadrangle for the Saddle Mountain Burn,

On each plot, all seedling and trees were recorded, except as noted above. For P. albicaulis, a single regeneration site often had more than one seedling or tree; the actural number was determined by separating stems or trunks at ground level. In the Sleeping Child Burn, all P. albicaulis seedlings or trees were aged, as well as representative individuals of height classes per plot for other conifer species. In the Saddle Mountain Burn, height class representatives for all conifer species were aged on all plots but B_9 through B_{12}; only P. albicaulis and A. lasiocarpa were aged on these plots. We determined age by cutting seedlings or small trees at ground level and then counting rings with a hand lens. The trees taller than 2 m (mostly P. contorta) were cored at breast height. The ages of these were calculated by increasing breast height age by standard values: P. contorta - 5 years, A. lasiocarpa - 10 years, P. engelmannii - 10 years (S. F. Arno, pers. commun.).

Statistical analysis

For some comparisons between two samples, non-parametric statistics were used because parametric assumptions concerning random sampling, normal distribution, and homogeneity of variance were not always met (Siegel 1956). In some cases the assumptions were met or the independent sampling and sample sizes were adequate for regression analysis. The slopes and intercepts of regression models were compared statistically using the methods of Greybill (1976). The P. albicaulis density for plot A_9 (.086 sites/m^2) was excluded from the data analysis, because it was almost an order of magnitude higher

than other P. albicaulis densities on the flatter, northeastern part of the transect. All analyses for the Sleeping Child Burn were conducted on a microcomputer with Microstat (version 4.1, Ecosoft, Inc.), and all analyses for the Saddle Mountain Burn and comparisons between burns were conducted on a VAX, using SPSS.

RESULTS

Sleeping Child Burn

The unburned forest at the northeastern edge of the burn is co-dominated by P. albicaulis and A. lasiocarpa (Table 1). The understory of the steep (45°) north aspect (40°) plot consisted of Vaccinium, Menziesia, Lonicera, Xerophyllum, Carex and Arnica. P. albicaulis ranged in dbh from less than 3 cm to 53 cm, and about 38% of the trees were 3 cm or smaller in dbh, perhaps indicating on-going regeneration. However, two trees of less than 3 cm dbh proved to be 70 and 85 years old, suggesting that some small trees were restricted in growth by current conditions. One tree 26 cm in dbh was 179 years old. A. lasiocarpa ranged in dbh from less than 3 cm to 33 cm, with 48% of the trees smaller than 3 cm dbh. The oldest tree aged, 151 years old, was 24 cm in dbh.

The understory of the south aspect (210°) plot, which sloped 5 to 10°, was dominated by Xerophyllum, Vaccinium, Carex, Luzula, and Polygonum. The south-facing forest is more open than the north-facing forest. P. albicaulis ranged from less than 3 cm to 41 cm dbh, with the largest tree aged at 202 years. One-third of the trees were 3 cm or smaller, indicating good regeneration. P.

lasiocarpa ranged from less than 3 cm to 18 cm dbh (82 years old). Only 1 tree, or 9% was less than 3 cm dbh. The few P. contorta and P. engelmannii were 3 cm or smaller in dbh.

The sampling area for P. albicaulis on the ridge study area in the Sleeping Child Burn totaled 15,475 m^2, and the sampling area for each of the other conifers totaled 12,225 m^2. For only 14 of the 63 plots, the sampling areas differed between P. albicaulis and each of the other conifers. For the road study area, the sampling area for P. albicaulis totaled 2975 m^2 and for each of the other conifer species, 1176 m^2.

For the ridge study area, P. albicaulis had the highest mean regeneration density per plot and the highest density of any plot (Table 2). At 48% of the 455 P. albicaulis regeneration sites, seedlings or trees occurred in clusters of 2 to 8, with a mean and standard deviation (S.D.) of 1.91 and 1.29, respectively. P. contorta regeneration density was next highest, and both A. lasiocarpa and P. engelmannii mean plot densities were an order of magnitude smaller. A comparison of plot densities between P. albicaulis and A. lasiocarpa indicated that the former were significantly greater than the latter (Mann-Whitney U test, U = 665.5, P < .00001).

The order of ranking of regeneration densities on the road study area was different (Table 2). A. lasiocarpa had the highest mean plot density and the highest plot density, which were ten and one hundred times the mean plot density and highest plot density, respectively, for P. albicaulis, the least dense species. The mean cluster size for P. albicaulis was 2.49 (S.D. = 2.05), with clusters of 2 to 9 at 49% of the regeneration sites. P. contorta had the

second highest regeneration density, followed by P. engelmannii.

Regeneration in the study areas began within two years of the fire. Ages for the oldest trees recorded for each species on the ridge study area were 21 years for P. albicaulis, 24 years for A. lasiocarpa and P. contorta, and 20 years for P. engelmannii. On the road study area, ages for the oldest trees were 19 years for P. albicaulis, 25 years for A. lasiocarpa, 15 years for P. contorta (only a few were aged), and 21 years for P. engelmannii.

For the ridge study area, scatterplots of plot densities vs. distance from the P. albicaulis seed source (upper, unburned forest) indicated interesting differences in regeneration patterns among the conifer species (Fig. 3). P. contorta densities increased significantly with increasing distance from the P. albicaulis seed source and, thus, with decreasing distance from both regenerated lower elevation P. contorta stands and lower elevation unburned forest (Table 3). Except for one anomalously high plot density at 3.65 km and a dip at 3 km (Fig. 3), the P. engelmannii scatterplot was nearly flat in profile. Although the regression analysis of density vs. distance was not significant, a positive relationship was indicated (Table 3). For A. lasiocarpa, the scatterplot indicated a statistically significant negative relationship between density and distance (Table 3), i.e., densities decreased as distances increased. The scatterplot for P. albicaulis was a pronounced negative exponential curve, with a long tail of low densities beginning at about 2 km; and, the regression analysis was highly significant (Table 3). Regression analysis also indicated a significant relationship between P. albicaulis plot density and elevation ($r = .608$, $df = 61$, $P < .001$). Unfortunately, the confounding effects of

elevation cannot be statistically separated from the influence of distance. Also, for all statistically significant regression analyses, r^2 values (Table 3) indicated that much variation was accounted for by factors in addition to the density vs. distance relationship.

For the road study area, all density vs. distance relationships were not significant (Table 3) because of the small number of plots. P. albicaulis again showed a negative relationship between density and distance from the seed source. In fact, the mean P. albicaulis plot density on the road study area was the same order of magnitude as the mean plot value on the ridge study area (Tomback et al. 1989), indicating good, long-distance dispersal from the seed wall. P. contorta, A. lasiocarpa, and P. engelmannii density increased with increasing distance from the P. albicaulis seed source and decreasing distance from the lower elevation forest.

For the ridge study area, a more meaningful regression analysis of P. albicaulis density vs. distance from the seed source was based on $\log_{10}$ density, which results in a highly significant linear relationship ($r = -.692$, $r^2 = .479$, $df = 61$, $P < .001$). This relationship is described by the model

$$\log_{10}Y = -0.0005X - 0.806.$$

With this model, an equation may be formulated to describe the negative exponential regeneration curve for P. albicaulis:

$$Y = (0.156)\ (10)^{-0.0005x}.$$

Saddle Mountain Burn

The east aspect plot (80°) had a slope of about 5° and an

understory of Xerophyllum, Lupinus, Luzula, and Vaccinium. P. albicaulis and A. lasiocarpa co-dominated the stand, with P. contorta a minor component (Table 1). For P. albicaulis and A. lasiocarpa, more than 65% of the trees were less than 3 cm dbh, indicating on-going regeneration. In contrast to the small trees in the upper, unburned, mature forest adjacent to the Sleeping Child Burn, these small trees were relatively young, based on the few ages obtained (20, 25 yr). One tree of less than 3 cm dbh provided an age adjustment factor of 15 years (the difference in age derived from base cores vs. breast height cores). Using theis factor, the oldest tree, with a dbh of 28 cm, was 104 years old. The oldest A. lasiocarpa, with a dbh of 26 cm, was about 86 years old.

The level, mountaintop plot had an understory of Xerophyllum, Luzula, and Carex. A. lasiocarpa had the highest density on this plot (Table 1), primarily because of abundant clonal growth. For P. albicaulis and A. lasiocarpa, 54% and 77%, respectively, of the trees were under 3 cm in size. Many groups of small A. lasiocarpa clustered around larger trees. The oldest P. albicaulis aged was 93 years old (dbh = 30 cm), and the oldest A. lasiocarpa was 120 years old (dbh = 36 cm). A P. contorta of 55 cm dbh was, at 174 years, the oldest tree on the plot.

The total area sampled for regeneration in the Saddle Mountain Burn differed for each conifer species, ranging from 1170 m^2 for P. contorta to 10,410 m^2 for P. albicaulis (Table 2). For statistical comparison, P. albicaulis and A. lasiocarpa regeneration was sampled on identical areas for 27 plots.

P. contorta regeneration dominated the Saddle Mountain Burn, with both the highest mean plot density and highest plot density (Table

2). P. albicaulis and A. lasiocarpa, comparable in densities, were the second most common conifers but a factor of 10 lower in density than P. contorta. At 43% of the 164 P. albicaulis sites, regneration was in clusters of 2 to 10 seedlings or trees, with a mean and S. D. of 1.98 and 1.62, respectively, per site. The mean plot densities of the least common conifers, P. engelmannii and P. menziesii, were the same order of magnitude as P. albicaulis and A. lasiocarpa, with overlap in plot densities. A statistical comparison of densities between P. albicaulis and A. lasiocarpa for plots with equal sampling area indicated no significant difference (Mann-Whitney U test, corrected for ties, $Z = -.286$, $P = .775$).

With respect to tree ages, regeneration appeared to begin 6 years after the fire. The oldest trees aged were 21 years for P. albicaulis, 16 years for A. lasiocarpa, 17 years for both P. contorta and P. menziesii, and 22 years for P. engelmanii.

The scatterplots of plot density vs. distance from the P. albicaulis seed source indicated patterns similar to those of the Sleeping Child Burn. Again, P. contorta densities increased with increasing distance from the upper seed source and decreasing distance from the lower elevation forest (Table 3). Flat in profile, the P. engelmannii curve spiked in density between 1.7 and 2.1 km; the relationship between density and distance was not significant. P. menziesii density increased with increasing distance from the upper seed source, although the regression analysis indicated a non-significant relationship Table 3). The scatterplot for A. lasiocarpa (Fig. 4) indicated a negative relationship between density and distance that was statistically significant (Table 3). For P. albicaulis, regeneration followed a negative exponential curve, as in

the Sleeping Child Burn (Fig. 4). The regression analysis indicated a highly significant relationship (Table 3), although the linear model based on $\log_{10}$ density was barely significant ($r = -.301$, $r^2 = .091$, $df = 38$, $P = .059$):

$$\log_{10}Y = -0.0002X - 1.065.$$

The model for the negative exponential regeneration curve is

$$Y = (0.086)(10)^{-0.0002x}.$$

Again, the effects of distance and elevation could not be statistically separated (density vs. elevation, $r = .884$, $r^2 = .781$, $df = 38$, $P < .0001$). Also, r^2 values for regression tests again indicate that factors in addition to distance affected conifer densities.

Comparisons between the burns

Because almost the same number of years elapsed between fire and our regeneration sampling in both burns, we compared *P. albicaulis* and *A. lasiocarpa* densities between both burns. First of all, *P. albicaulis* mean plot densities were of the same order of magnitude for both burns. Statistical comparison, in fact, indicated no significant difference in *P. albicaulis* plot densities between the burns (Mann-Whitney U test, corrected for ties, $Z = -.678$, $P = .498$, two-tailed). In contrast, the *A. lasiocarpa* mean plot density was an order of magnitude greater for the Saddle Mountain Burn. Saddle Mountain Burn *A. lasiocarpa* plot densities were indeed significantly higher than those of the Sleeping Child Burn (Mann-Whitney U test, corrected for ties, $Z = -4.29$, $P < .00001$). We remind the reader that each statistical comparison was based on different sampling

areas.

The slopes and intercepts of the linear models based on $\log_{10}$ P. albicaulis density vs. distance from the seed source were compared for both burns. There were no significant defferences between the models.

DISCUSSION

Prior studies of post-fire regeneration of bird-dispersed pines (Lanner and Vander Wall 1980, Tomback 1986) focused on relatively small areas and did not examine the pattern of regeneration with respect to potential seed sources. By examining two large burns of similar age and topography, we elucidated several general patterns concerning the regeneration of P. albicaulis and its forest associates in western Montana.

We determined that P. albicaulis regeneration was indeed widespread in the study burns. The seed source forest for P. albicaulis in both the Sleeping Child Burn and Saddle Mountain Burn was co-dominated by P. albicaulis and A. lasiocarpa, with one-third or more of the trees cone-bearing in size. It is likely that both seed source forests were predominantly of the timberline habitat type classified as Pinus albicaulis - Abies lasiocarpa (Pfister et al. 1983), which is a climax association. However, the habitat type of the north slope plot of the Sleeping Child Burn was likely to be Abies lasiocarpa/Luzula hitchcockii, of which P. albicaulis is a seral component (Pfister et al. 1983).

Regeneration patterns

The regeneration patterns of P. albicaulis differed in several respects from that of the other conifers. First of all, nearly half of the regeneration was in clusters of 2 to 10 seedlings or trees per site in both burns, a direct consequence of the tendency of nutcrackers to bury more than one seed at a site (e.g., Tomback 1978). Secondly, regeneration density vs. distance from the P. albicaulis seed wall followed a distinct, negative exponential distribution. Regeneration data collected in the road study area of the Sleeping Child Burn indicated that the tail of this distribution continued for at least 8 km, a consequnce of nutcrackers transporting seeds to distant storage sites. Nutcracker activity, in fact, appeared comparable in both burns, assuming equal seed sources, because the P. albicaulis plot densities did not differ significantly.

The confounding effects of distance from the P. albicaulis seed source and elevation could not be separated. However, P. albicaulis grows well at elevations of 2100 m and above in the Bitterroot National Forest (Arno 1986, Arno and Hoff 1989). Therefore, elevation was not likely to affect regeneration greatly in the study areas.

The regeneration pattern of A. lasiocarpa was similar to that of P. albicaulis, because it also showed a negative relationship between density and distance from the upper, unburned forest This suggested that the primary seed source for A. lasiocarpa was the upper forest. However, for the road study area of the Sleeping Child Burn, the pattern was reversed; regeneration density became greater with decreasing distance from the lower elevation forest. Thus, both the

upper and lower elevation forests probably provided A. lasiocarpa seeds.

Prior to the fire, P. contorta dominated the lower subalpine forest of both burns (e.g., Lyon and Stickney 1976, Lotan 1976). Restocking of these areas probably resulted, in part, from seeds from serotinous cones on site (Lotan 1976). During our studies, throughout both burns, young P. contorta were already producing cones and acting as a secondary seed source, as indicated by the groups of seedlings around parent trees. As a consequence, the regeneration curves of P. contorta in all study areas indicated a positive relationship between density and distance from the P. albicaulis seed source, i.e., density increased with decreasing distance to the lower elevation forest and regenerating stands of P. contorta.

The regeneration patterns of P. engelmannii and P. menziesii similarly showed a positive relationship between density and distance from the upper forest, suggesting that the lower elevation forest was the primary seed source for these species. The scatterplot for P. engelmannii in the road study area further supported this suggestion.

Tree ages suggested that regeneration began in different years for the conifer species, both within and between burns. This makes sense, because large cone crops tend to be produced at different intervals and often asynchronously among species. Initiation of regeneration for all species but P. contorta depends on when a cone crop occurs; P. contorta may be regenerated by seeds from serotinous cones following fire.

Pinus albicaulis regeneration models

The linear models based on $\log_{10}$ density that described P. albicaulis regeneration in the Sleeping Child Burn and the Saddle Mountain Burn were statistically similar. They are potentially useful for predicting regeneration patterns for simulations or mangement applications. Such uses are currently of importance with respect to losses of P. albicaulis populations and seed sources from advancing succession, epidemics of mountain pine beetles, and blister rust. The model for the Sleeping Child Burn has already been incorporated into a forest process model for P. albicaulis regeneration simulations (Keane et al. 1989a, Keane et al. 1989b).

Pinus albicaulis vs. Abies lasiocarpa

A. lasiocarpa is the climax species of the Abies lasiocarpa/Luzula hitchcockii habitat type of the upper subalpine zone of western Montana (Pfister et al. 1983), replacing P. albicaulis over time. Although P. albicaulis is a pioneer, whether it always has a strong, initial regeneration advantage in burns over A. lasiocarpa is unknown. In the Sleeping Child Burn, P. albicaulis regeneration densities were significantly greater than those of A. lasiocarpa 26 years after fire. Because the unburned upper forest, the primary seed source for both species in the ridge study area, supports equal densities of P. albicaulis and A. lasiocarpa, seed availability for regeneration has probably been similar for both species. Thus, the advantage to P. albicaulis must come from seed dispersal by nutcrackers.

If the prevailing winds are unfavorable to a wind-dispersed conifer, seed dispersal by nutcrackers may be particularly

advantageous. The prevailing winds in the region during the time that conifers release seeds are from the west (Finklin 1983, A.I. Finklin, pers. commun.), and the direction that A. lasiocarpa seeds must travel is from the northeastern forest towards the west into the burn. This fact could account for the higher densities of P. albicaulis on the ridge study area. In addition, seed dispersal by nutcrackers, which can be over long distances, may be advantageous in a very large burn like the Sleeping Child Burn. The maximum seed dispersal distances of wind-dispersed conifers are typically under 500 m (McCaughey et al 1986).

The Saddle Mountain Burn provides a test of the hypotheses that unfavorable prevailing winds and that a very large burn result in lower regeneration densities of wind-dispersed conifers. The prevailing winds from the west blow seeds east into the burn from the forest at the southwestern edge. This and the smaller size of the burn probably result in a higher density of A. lasiocarpa seeds avai for regeneration. The densities of A. lasiocarpa in the Saddle Mountain Burn were, in fact, significantly greater than those in the Sleeping Child Burn, although no statistical difference in P. albicaulis densities occurred between the two burns. Relative differences in P. albicaulis and A. lasiocarpa densities in the upper, unburned forest of the Saddle Mountain Burn are unlikely to account for greater A. lasiocarpa densities. Although the density of A. lasiocarpa was much higher than that of P. albicaulis on the mountaintop plot (Table 1), a high percentage of A. lasiocarpa trees were under 3 cm dbh and, thus, not cone-bearing.

Thus, the comparison of regeneration patterns between the two burns suggests that P. albicaulis, a bird-dispersed pine, may have distinct

advantages over A. lasiocarpa under circumstances where 1) the burned area is very large and seed dispersal by nutcrackers typically extends over greater distances than does seed dispersal by wind, 2) prevailing winds are against the direction of the burn, and, by extrapolation, 3) a seed source is more than a kilometer from the perimeter of the burn.

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LITERATURE CITEE

Arno, S. F. 1980. Forest fire history in the northern Rockies. Journal of Forestry 78:460-465.

Arno, S. F. 1986. Whitebark pine cone crops--a diminishing source of wildlife food? Western Journal of Applied Forestry 1:92-94.

Arno, S. F., and R. J. Hoff. 1989. Silvics of whitebark pine (Pinus albicaulis). United States Forest Service Intermountain Forest and Range Experiment Station Research Paper INT-253.

Arno, S. F., and T. D. Petersen. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. United States Forest Service Intermountain Forest and Range Experiment Station Research Paper INT-301.

Finklin, A. I. 1983. Weather and climate of the Selway-Bitterroot Wilderness. University Press of Idaho, Moscow, Idaho, USA.

Furnier, G. R., P. Knowles, M. A. Clyde, and B. P. Dancik. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution 41:607-612.

Greybill, F. A. 1976. Theory and application of the linear model. Duxbury Press, North Scituate, Massachusetts, USA.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192-201.

Keane, R. E., S. F. Arno, J. K. Brown, and D. F. Tomback. 1989a. Modelling stand dynamics in whitebark pine forests. Ecological Modelling, in press.

Keane, R. E., S. F. Arno, J. K, Brown, and D. F. Tomback. 1989b. Modelling disturbances and conifer succession in whitebark pine

forests. Pages in Proceedings--Whitebark pine ecosystems: ecology and management of a high mountain resource. United States Forest Service Intermountain Forest and Range Experiment Station, in press.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. Pages 166-173 in Bears--their biology and management, Vol. 5. International Association of Bear Management, Calgary, Alberta, Canada.

Kendall, K. C., and S. F. Arno. 1989. Whitebark pine: an important but endangered food for wildlife. Pages in Proceedings--Whitebark pine ecosystems: ecology and management of a high mountain resource. United States Forest Service Intermountain Forest and Range Experiment Station, in press.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Pages 14-48 in Proceedings of Sixth North American Forest Biology Workshop, University of Alberta, Edmonton, Alberta, Canada.

Lanner, R. M., and S. B. Vander Wall. 1980. Dispersal of limber pine seed by Clark's Nutcracker. Journal of Forestry 78:637-639.

Lotan, J. E. 1976. Cone serotiny--fire relationships in lodgepole pine. Pages 267-278 in Proceedings Tall Timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council Fire and Land Management Symposium, Tallahassee, Florida, USA.

Lyon, L. J., and P. F. Stickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. Pages 355-375 in Proceedings Tall timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council Fire and Land Management Symposium, Tallahassee, Florida, USA.

McCaughey, W. W., W. C. Schmidt, and W. C. Shearer. 1986. Seed-dispersal characteristics of conifers in the Inland Mountain West. Pages 50-62 in Proceedings--Conifer tree seed in the Inland Mountain West Symposium, United States Forest Service Intermountain Forest and Range Experiment Station General Technical Report INT-203.

Pfister, R. D., B. L. Kovalchik, S. Arno, and R. Presby. 1977. Forest habitat types of Montana. United States Forest Service Intermountain Forest and Range Experiment Station General Technical Report INT-34.

Romme, W. H. 1980. Fire frequency in subalpine forests of Yellowstone National Park. Pges 27-30 in Proceedings of Fire History Workshop. United States Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report RM-81.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.

Smith, C. C., and R. P. Balda. 1979. Competition among insects, birds, and mammals for conifer seeds. American Zoologist 19: 1065-1083.

Sund, S. K. 1988. Post-fire regeneration of Pinus albicaulis in western Montana: patterns of occurrence and site characteristics. Thesis. University of Colorado at Denver, Denver, Colorado, USA.

Sund, S. K., D. F. Tomback, and L. A. Hoffman. Post-fire regeneration of Pinus albicaulis in western Montana: patterns of occurrence and site characteristics. Manuscript.

Tomback, D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16:123-161.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: a mutualism hypothesis. Journal of Animal Ecology 51:451-467.

Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? Pages 179-223 in N. H. Nitecki, ed. Coevolution. University of Chicago Press, Chicago, Illinois, USA.

Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono 33: 100-110.

Tomback, D. F., L. A. Hoffman, and S. K. Sund. 1989. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. Pages in Proceedings--Whitebark pine ecosystems: ecology and management of a high mountain resource. United States Forest Service Intermountain Forest and Range Experiment Station, in press.

Turcek, F. J., and L. Kelso. 1968. Ecological aspects of food transportation and storage in the Corvidae. Communications in Behavioral Biology. Part A 1:277-297.

TABLE 1. Conifer densities (sites/m^2) in plots of unburned upper forest adjacent to burns (see text for details). n is the number of tree sites. PIAL = Pinus albicaulis, ABLA = Abies lasiocarpa, PICO = Pinus contorta, PIEN = P. engelmannii.

Location	PIAL	ABLA	PICO	PIEN
Sleeping Child Burn				
North plot				
	.090	.080	--	--
	n = 45	n = 40		
South plot				
	.038	.022	.004	.002
	n = 19	n = 11	n = 2	n = 1
Saddle Mountain Burn				
East plot				
	.104	.116	.024	--
	n = 47	n = 52	n = 11	
Top plot				
	.123	.380	.010	--
	n = 37	n = 114	n = 3	

TABLE 2. Conifer regeneration plot densities (sites/m^2) for the Sleeping Child Burn and the Saddle Mountain Burn. See Table 1 for species abbreviations. PSME = Pseudotsuga menziesii, S.D. = standard deviation.

		PIAL	ABLA	PICO	PIEN	PSME
Sleeping Child Burn, Ridge study area						
No. of tree sites		455	60	436	37	--
Tree density:	Range	0-.512	0-.080	0-.296	0-.056	--
	Mean	.070	.008	.040	.004	--
	S.D.	.104	.001	.066	.009	--
Sleeping Child Burn, Road study area						
No. of tree sites		45	123	80	38	--
Tree density:	Range	0-.067	0-1.69	0-1.04	0-.58	--
	Mean	.021	.396	.241	.124	--
	S.D.	.020	.539	.277	.183	--
Saddle Mountain Burn						
No. of tree sites		164	175	286	49	29
Area sample m^2		10,410	5980	1580	1170	1580
Tree density:	Range	0-.160	0-.280	0-1.24	0-.200	0-.160
	Mean	.042	.046	.323	.030	.019
	S.D.	.051	.068	.355	.044	.032

TABLE. 3. Regression analyses of plot density vs. distance from the upper, unburned forest (P. albicaulis seed source). r = Pearson correlation coefficient, df = degrees of freedom, NS = non-significant, P = probability. See Tables 1 and 2 for keys to species abbreviations.

	r	r^2	df	P
Sleeping Child Burn, Ridge study area				
PICO	.482	.232	61	< .001
ABLA	-.355	.126	61	.01 > P > .001
PIEN	.187	.035	61	NS
PIAL	-.592	.351	61	< .001
Sleeping Child Burn, Road study area				
PICO	.188	.035	12	NS
ABLA	.250	.062	12	NS
PIEN	.340	.116	12	NS
PIAL	-.374	.140	12	NS
Saddle Mountain burn				
PICO	.320	.103	29	.079
ABLA	-.498	.248	39	.001
PIEN	.021	.000	29	NS
PSME	.170	.029	29	NS
PIAL	-.822	.676	38	< .0001

LEGENDS

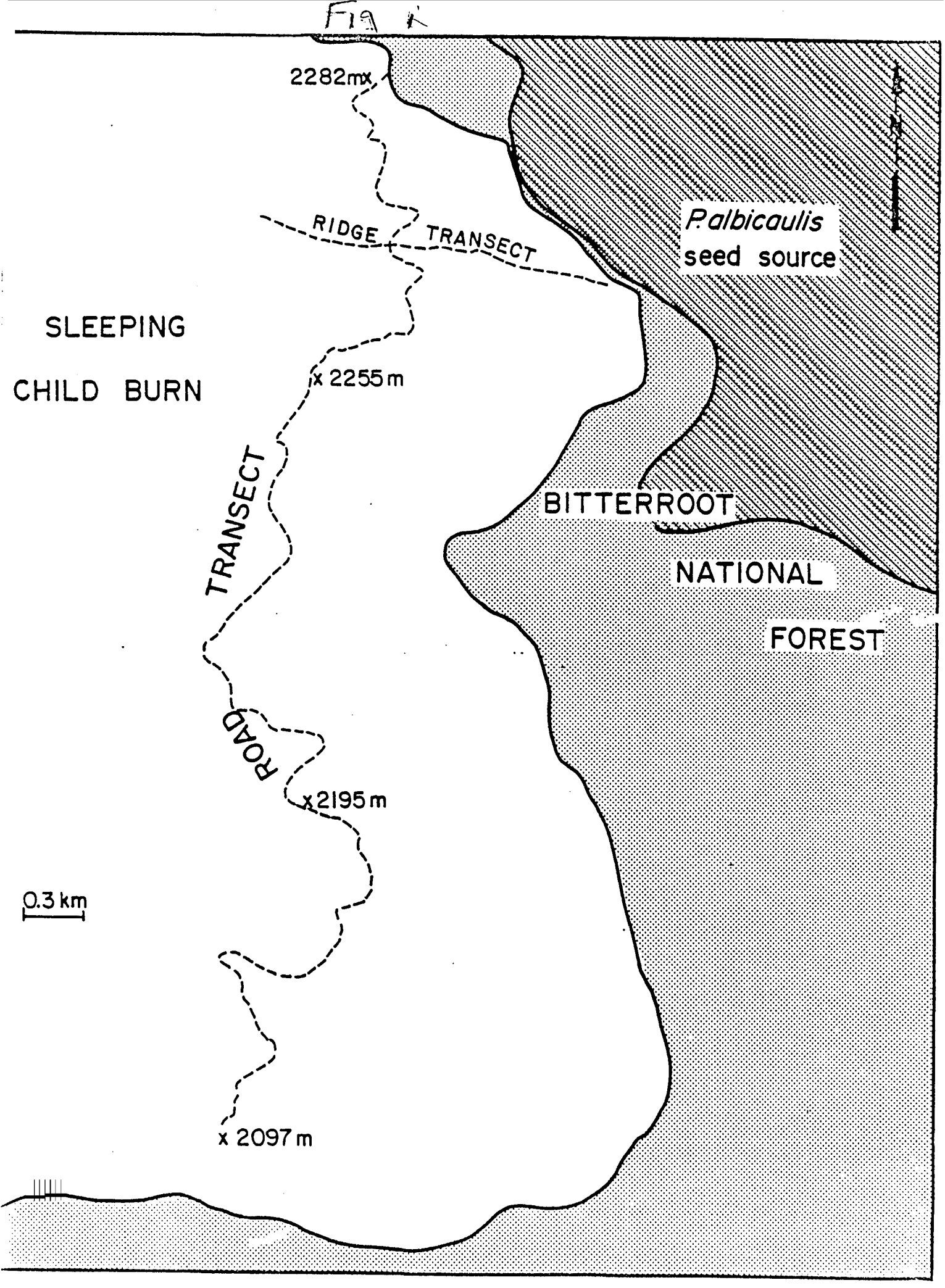
Fig. 1. Sleeping Child Burn ridge and road study areas, Bitterrrot National Forest, western Montana. The dark, striped area indicates forest above 2250 m elevation where continuous stands of P. albicaulis provide seeds for regeneration.

Fig. 2. Saddle Mountain burn, Bitterroot National Forest, western Montana. Path of parallell A and B transects through the burn. The dark, striped area indicates forest above 2250 m where continuous stands of P. albicaulis provide seeds for regeneration. The stippled area indicates lower elevation, unburned forest around the perimeter of the burn. On the inset graph of elevation vs. aerial distance from the upper, unburned forest, each point represents a single plot (n = 41).

Fig. 3. For the ridge study area of the Sleeping Child Burn, scatterplots of regeneration density vs. distance from the upper, unburned forest (P. albicaulis seed source) for four conifer species.

Fig. 4. For the Saddle Mountain Burn, scatterplots of regeneration density vs. distance from the upper, unburned forest (P. albicaulis seed source) for P. albicaulis and its competitor A. lasiocarpa.

Fig 1


2282m
RIDGE TRANSECT
P.albicaulis
seed source
SLEEPING
CHILD BURN
x 2255 m
TRANSECT
BITTERROOT
NATIONAL
FOREST
ROAD
x 2195 m
0.3 km
x 2097 m

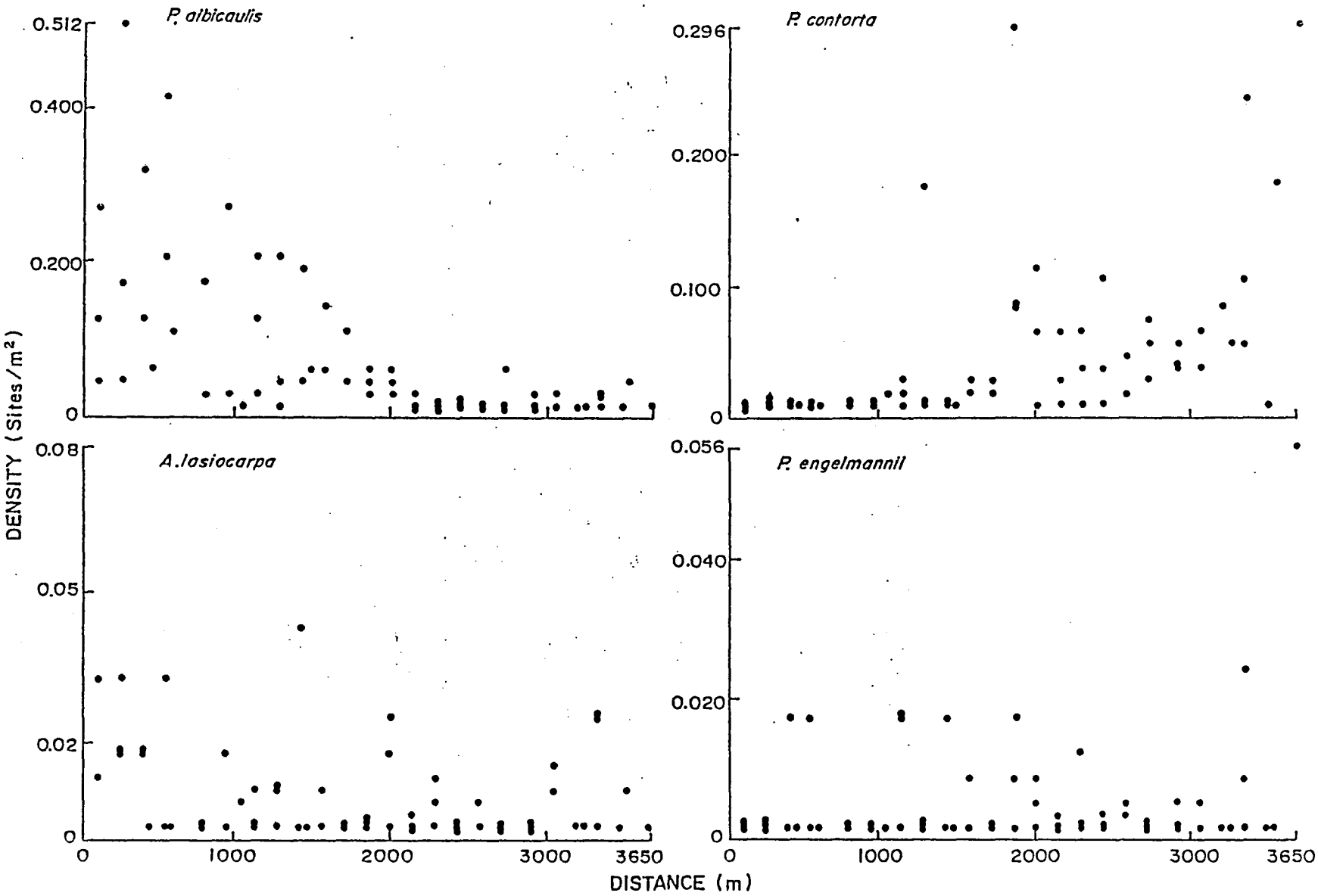

P. albicaulis
P. contorta
A. lasiocarpa
P. engelmannii
DENSITY (Sites/m²)
DISTANCE (m)
0.512
0.400
0.200
0
0.296
0.100
0.08
0.05
0.02
0.056
0.040
0.020
1000
2000
3000
3650

Fig 3

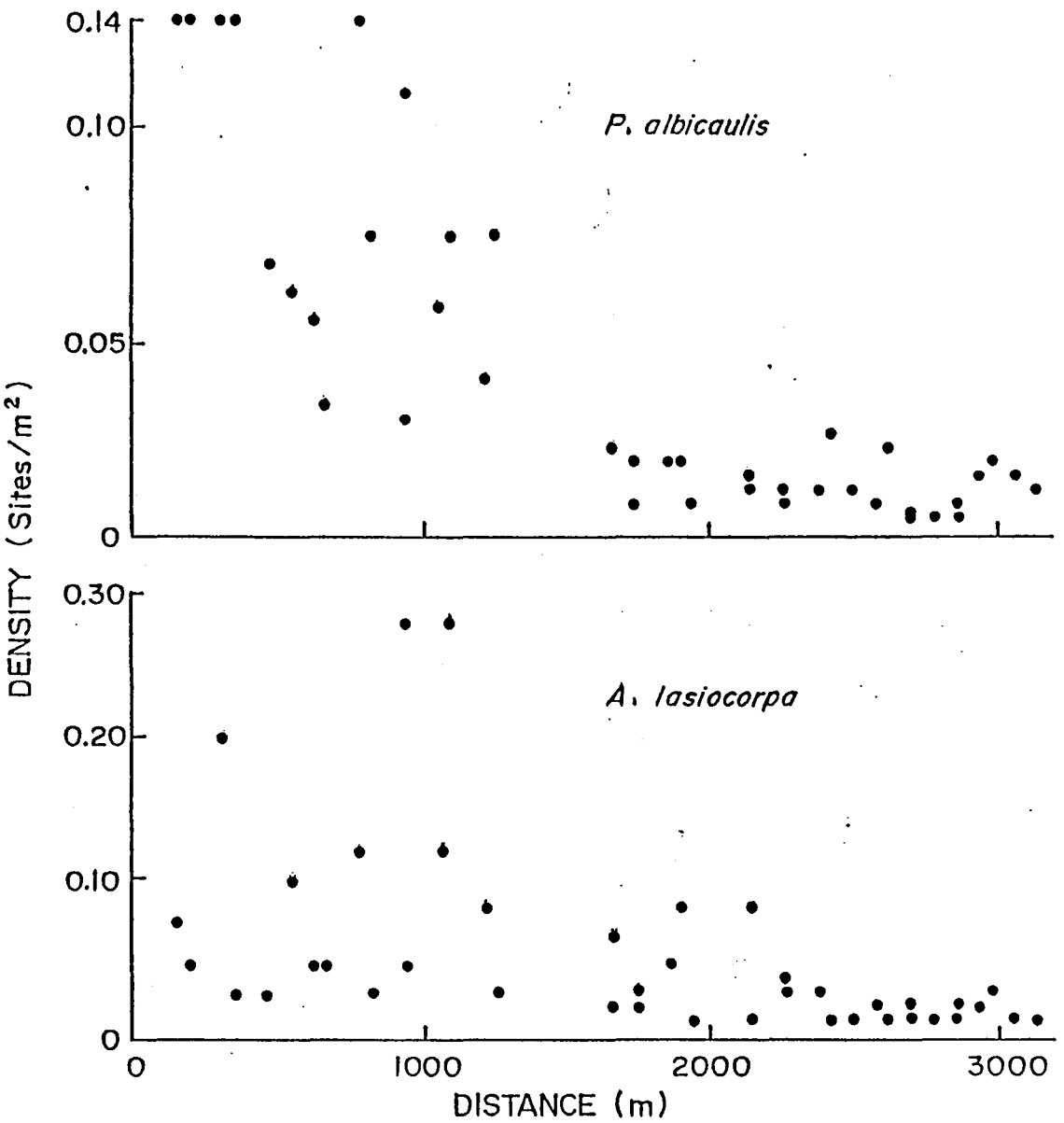

0.14
0.10
0.05
0
P. albicaulis
0.30
0.20
0.10
0
A. lasiocorpa
DENSITY (Sites/m²)
0
1000
2000
3000
DISTANCE (m)

Fig. 4

Running Head: Post-fire regeneration of *Pinus albicaulis*

POST-FIRE REGENERATION OF **PINUS ALBICAULIS** IN WESTERN MONTANA: PATTERNS OF OCCURRENCE AND SITE CHARACTERISTICS

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Abstract. In the summer of 1961, the severe Sleeping Child fire in the Bitterroot National Forest, western Montana, destroyed about 11,350 hectares of subalpine forest. The upper elevations of this burned forest (above about 2200 m) contained Pinus albicaulis (whitebark pine). Because of recent concern about declining abundance of P. albicaulis, a major subalpine component of the northern Rocky Mountains (Arno 1986, Kendall and Arno 1989), healthy regeneration of P. albicaulis in the burn is an important concern. Unlike most pines, P. albicaulis relies on a bird, Clark's nutcracker (Nucifraga columbiana), for seed dispersal. In 1987, forest regeneration within the Sleeping Child Burn was studied on 77 plots along two transects: 1) an east-west ridge exhibiting a gradient for both elevation (range 2148 m to 2182 m) and distance from a P. albicaulis seed source (range 50 m to 3650 m) (n = 63 plots), and 2) a north-south transect of greater distance from a seed source but maintaining relatively constant elevation (n = 14 plots).

Regeneration patterns indicated that nutcrackers have dispersed clusters ranging from one to nine P. albicaulis seeds 8 km or more into the burn. On the ridge transect, a significant negative correlation was found between P. albicaulis regeneration density and distance from seed source. A significant positive correlation was also found between density and elevation; it was not possible to separate the effects of elevation and distance. Neither of these correlations were significant on the north-south transect.

Regeneration patterns show that Pinus albicaulis and Pinus contorta are dominating the post-fire succession on the east-west ridge. The regeneration status of P. albicaulis in the Sleeping Child Burn indicates an advantage over its associates, Abies lasiocarpa and Picea engelmannii, and perhaps a return to the successional upper subalpine forest communities that were widespread prior to the fire suppression policies of this century.

Key words: Montana, Nucifraga columbiana, Pinus albicaulis, post-fire regeneration, post-fire succession, seed dispersal, bird-dispersed plants.

Topic sentences: post-fire regeneration of a bird-dispersed pine, site characteristics of Pinus albicaulis, regeneration patterns of Pinus albicaulis.

INTRODUCTION

Recently, surveys indicate that Pinus albicaulis (whitebark pine), a major component of subalpine forests in the northern Rocky Mountains, is declining in some large areas (Arno 1986, Kendall and Arno 1989). Losses result from advancing forest succession enhanced by a combination of fire suppression practices and epidemics of insects and disease. Although not an important timber species, P. albicaulis is now recognized as a valuable food source for wildlife because of its nutritious seeds (Tomback 1978; Kendall 1980a,b; Hutchins and Lanner 1982; Arno 1986). Also, it is the only North American member of the Cembrae

subsection of the Strobus pines; species of this subsection are characterized by indehiscent cones and large, wingless seeds (Mirov 1967; Mirov and Hasbrouck 1976). All Cembrae pines are dependent upon birds of the genus Nucifraga ("nutcrackers") for seed dispersal (Lanner 1980; Tomback 1983).

Fires have played an important ecological role in the perpetuation of P. albicaulis, with low-intensity surface fires allowing the tree to regenerate in small openings and severe, stand-replacing fires giving P. albicaulis regeneration an initial advantage over its shade-tolerant competitors Abies lasiocarpa and Picea engelmannii (Arno 1986, Arno and Hoff 1989). Fire suppression beginning in the early 1900's has limited the size of wildfires and lengthened fire-free intervals, thus reducing the rate at which P. albicaulis is rejuvenated (Arno 1986). In addition, infestations of mountain pine beetle (Dentroctonus ponderosae) have destroyed hundreds of thousands of hectares of mature P. albicaulis forests in the northern Rockies since 1904 (Arno 1986). Mature stands of P. albicaulis and its associate Pinus contorta are favored by mountain pine beetles, and such stands have become extensive and contiguous on the landscape with longer fire intervals. A disease introduced from Europe, white pine blister rust (Cronartium ribicola), is also a serious threat to P. albicaulis in cool, moist mountain regions such as in northwestern Montana, northern Idaho, and Washington (Arno 1986, Arno and Hoff 1989).

We studied the regeneration of P. albicaulis 26 years after a

severe fire in 1961 killed over 11,000 hectares of subalpine forest in the Sapphire Range, southeast of Hamilton, Montana. The patterns of P. albicaulis regeneration and competition from Abies lasiocarpa and Picea engelmannii are of interest to forest managers who are concerned about declining vigor and abundance of P. albicaulis.

Pinus albicaulis

Unless indicated otherwise, the following information is summarized from Arno (1986) and Arno and Hoff (1989). P. albicaulis is a haploxylon (soft) pine that ranges from British Columbia south to central California and east to western Wyoming, occurring on exposed slopes and ridges of high mountains. Found only at timberline in the north end of its distribution, P. albicaulis increases in abundance at both timberline and upper subalpine as latitude decreases. In west-central Montana, it is a major component of high elevation forests and the timberline zone (between 2130 and 2830 meters). The boundary between the lower and upper subalpine zones is considered to be the lower limit of P. albicaulis as a major component of the forest (Pfister et al. 1977). This slow growing, long-lived (as much as 1000 years) conifer reaches heights of 12 - 30 meters in the upper subalpine zone and often exhibits a multi-trunk growth form. P. albicaulis occurs on coarse, rocky soils in climatic zones characterized by short, cool summers and cold, snowy

winters. In mesic mountain ranges it is restricted to warm dry exposures, while in semi-arid mountains it is more abundant on cool, moist slopes.

Principally a seral component of mixed coniferous forest in the upper subalpine, and a pioneer on recently burned or disturbed sites, P. albicaulis is also a climax species on xeric sites and on harsh sites at timberline (Fischer and Bradley 1987). In the Rocky Mountains Pinus albicaulis usually associates with Abies lasiocarpa, Picea engelmannii, and Larix lyallii at high elevations bordering timberline (Wright and Bailey 1982), and also with Pinus contorta in the lower part of its distribution on the mountains. At timberline, P. albicaulis, P. engelmannii, and A. lasiocarpa may end up as climax co-dominants (Arno and Hoff 1989). But in most subalpine areas, P. albicaulis is eventually replaced by A. lasiocarpa with P. engelmannii and P. contorta as minor components. P. albicaulis is considered to be less shade-tolerant than A. lasiocarpa or P. engelmannii but more tolerant than P. contorta.

As a successional species in subalpine communities, P. albicaulis is periodically regenerated by fire. The order of fire-resistance or tolerance is P. contorta > P. albicaulis > P. engelmannii > A. lasiocarpa (Fischer and Bradley 1987); Arno (personal communication) rates P. contorta and P. albicaulis equally fire tolerant. Dry exposed sites and open stands with light fuels offer P. albicaulis more protection from fire than does its moderately thin bark (Mirov 1967; Mirov and Hasbrouck

1976). P. albicaulis trees shed their lower branches as they grow, preventing vertical fuel continuity that can cause surface fires to become crown fires (Romme 1982).

Fire intervals in the Bitterroot National Forest during the 300 years prior to 1910 range from a mean of 40 to 100+ years in the upper subalpine where P. albicaulis is found. In contrast, much longer fire cycles occur as a result of fire suppression. This favors advancing succession to dominance by Abies lasiocarpa and Picea engelmannii.

Seed dispersal mechanisms

The majority of conifers have seeds that bear woody, membranous seed wings and are wind-dispersed. Whereas all cones of Abies lasiocarpa and Picea engelmannii open upon ripening to release seeds, only some cones of Pinus contorta disperse seed this way. Some P. contorta cones are serotinous and adhere to the tree for several years, until the heat of fire opens cones and broadcasts seeds (Lotan 1975, 1976). Wind-dispersed species generally exhibit a U-shaped seed distribution across forest openings, with the quantity of seeds dispersed being greatest at the windward and leeward edges of clearings and decreasing towards the center of the opening. The local dispersal curve shape for these three species is a negative exponential curve (McCaughey et al. 1986).

Pinus albicaulis, in contrast, is one of about eight pines in the world known to be dependent upon the family Corvidae for

dissemination (Lanner 1980; Tomback 1983). The cones do not open upon ripening (indehiscent), and they contain large, wingless seeds. Clark's nutcracker (Nucifraga columbiana) is the primary dispersal agent of P. albicaulis (Tomback 1982, 1983; Hutchins and Lanner 1982). After P. albicaulis seeds have ripened and hardened, nutcrackers pry whole seeds from the cones with their bills and transport the seeds in a sublingual pouch for distances of a few meters to 12.5 km (Tomback 1982). In fact, Vander Wall and Balda (1977) report nutcrackers carrying Pinus edulis (pinyon) seed distances of 22 km or further, and presumably this could apply to P. albicaulis seeds as well. Pouch contents can average 77 P. albicaulis seeds and as many as 150 (Tomback 1982). Nutcrackers disperse pine seeds by burying clusters or "caches" of seeds in the soil, from 1 - 15 seeds per site with a mean of 3.7; each bird may make 8,000 or more caches if the cone crop is good (Tomback 1982). Many of these seeds are retrieved by nutcrackers during winter and spring when other foods are scarce, but a large percent are also left unharvested and can germinate (Tomback 1982).

Bird dispersal affects the growth form of the trees and genetic structure of P. albicaulis populations (Linhart and Tomback 1985, Furnier et al. 1987). Multi-genotype tree clusters, often with trunks fused at the base, are common in P. albicaulis and a few other species dispersed by nutcrackers.

Hypotheses

1) Because Pinus albicaulis is a typical pioneer species of the subalpine in the Northern Rocky Mountains, this conifer should be a major component in the regenerating communities in the Sleeping Child Burn. 2) Because 26 years have elapsed since the fire, P. albicaulis regeneration should be advanced, with a range of age groups apparent. 3) With a localized P. albicaulis seed source, regeneration is expected to show a density gradient, with greatest density near the seed source. 4) The patterns of P. albicaulis regeneration should be consistent with patterns of avian seed dispersal.

METHODS

Study area

In the vicinity of The Sleeping Child Burn the upper subalpine forest, containing Pinus albicaulis, grows between 2130 m and 2440 m (Arno and Petersen 1983, Arno et al. 1985). Surface geologic formation is of granitic origin, with medium to coarse-textured, shallow, rocky soils; ancient wind-deposited volcanic ash and loess have resulted in the leeward slopes (north and east aspects) having deeper soil mantles (Arno et al. 1985). The nearest P. albicaulis seed source for the Sleeping Child Burn is considered to be the continuous stands of cone-bearing P. albicaulis that are contiguous with the burned area on the northeast border (Figures 1 and 2), since the other burn boundaries are below the usual elevation of P. albicaulis (Arno, personal communication). The habitat type groups for potential climax on upper subalpine slopes are 1) Abies lasiocarpa-P. albicaulis/Vaccinium scoparium and 2) A. lasiocarpa/Luzula hitchcockii, primarily in the burn. P. albicaulis-A. lasiocarpa is a timberline habitat type found perhaps at the top of the ridge transect (Pfister et al. 1977).

The south slopes are much warmer and drier, whereas north slopes experience less solar insolation, greater snow

accumulations and deeper soils - resulting in cooler, moister conditions (Pfister et al. 1977). Annual precipitation averages roughly 75 cm and varies with elevation and topography (USDA Soil Conservation Service 1977). Seventy percent of the precipitation above 2135 m is from snowfall (Lyon 1976). Winter and late spring are the wettest seasons; lightning activity during dry summer periods results in fires (Finklin 1983).

Field work was conducted from 3 to 26 August 1987 on two areas in the burn. The first study transect was located along an east-west ridge transect, 3.6 km long, from the edge of the burn heading west to approximately the northern center of the burn (Figure 1). The second transect was a 20.6 km length of north-south road transect following Skalkaho-Rye Road and Paint Creek Road, running approximately from the center of the burn to its southern edge (Figure 2).

Transect #1 - ridge

Plots were sampled at 150 m intervals on a 3.65 km transect along a straight ridge extending into the burn and away from the P. albicaulis seed source. The ridge gradually decreases in elevation at increasing distance from the unburned forest. Each ridgetop plot was paralleled by plots on the north- and south-facing slopes of the ridge, thus creating a triple transect: ridgetop sites, north-slope sites, south-slope sites. In a few instances a representative north or south aspect was not

available. A total of 63 plots were studied: 21 north, 19 south, and 23 ridge. All plots were oriented east-west longitudinally, with belt width measured south from the transect line. Size of the plots ranged from 50 x 1.25 m to 50 x 12 m. Belt width varied for the purpose of adequately characterizing densities of Pinus albicaulis regeneration. It was important to avoid zero densities and yet quickly process plots where densities were high. On the west end of the ridge, P. albicaulis regeneration was sparse, so belt width was increased to 10 m or 12 m. Narrower widths were used on the east end of the ridge where P. albicaulis densities were much higher. Belt widths for the other three conifer species (Pinus contorta, Abies lasiocarpa, and Picea engelmannii) were sometimes shorter than the belt widths for P. albicaulis.

For comparison with the burned area on the ridge study site, two plots, one on north and one on south aspects, were located in the adjacent unburned forest, at a distance of 150 m east of the first ridge plot. The north and south forest plots were at elevations of 2440 m and 2420 m, respectively, and each plot was 500 m^2 in area. All trees within these plots were counted.

Transect #2 - road

This second transect was selected to measure forest regeneration at fairly constant elevation and aspect but increasingly greater distances from the Pinus albicaulis seed

source. A total of 14 plots were studied on north-facing aspects along the Skalkaho-Rye Road and Paint Creek Road (Fig. 2). The plots were separated by road distances of 644 m to 2574 m, and their locations corresponded to aerial distances of 1 km to 8 km from the unburned forest. Plot sizes ranged from 30 x 1.5 m to 30 x 10 m. Plot width was determined by the density of the vegetation, and was expanded to include at least one *P. albicaulis* seedling per plot.

Field methods

Plot measurements included: major undergrowth species, elevation, percent slope, aerial distance from *Pinus albicaulis* seed source, aspect, and number of regeneration sites of all species. Evidence of post-fire disturbance such as grazing, thinning, woodcutting, etc. was noted. Because the seed source is considered to be the continuous stands of *P. albicaulis* that occur at elevations above 2257 m near the northeast edge of the burn, aerial distance from the boundary of the *P. albicaulis* seed source was measured on a topographic map to the nearest 10 m. The term 'site' is used to refer to a location with a cluster of one or more *P. albicaulis* trees. At each *P. albicaulis* site the following data were gathered: percent slope, aspect, identification of 1 to 4 vascular plant species found within 15 cm of the site, and the nearest object (rock, wood pieces or fallen snag, etc.) located within 15 cm. Cluster size was

recorded as the number of individual trunks at a single site and was determined by separating trunks to or below ground level.

The height of each individual tree was recorded, and a number of trees of every representative height category were aged. On all plots within the burn, tree age was determined by cross-sectioning the trunk at ground level and counting tree rings with a hand lens. Newly germinated trees were given a 0.5 year age value; all other ages were in whole years. Tree age on the unburned plots was determined by increment coring near the ground line and counting tree rings.

Statistical methods

Although a ratio scale of measurement was used for distance, elevation, and tree density data, non-parametric statistics were used in some analyses because underlying parametric assumptions concerning random sampling, normal population distributions, and homogeneity of variance were not always met. Our transects were systematically laid out to obtain plots at pre-determined orientations (east-west along an elevational gradient from center of burn to edge of burn, and north-south along a distance gradient from edge of burn). Normal population distributions were not indicated for P. albicaulis tree or site density on any transect, or for elevation on the north, ridge or south transects. Heterogeneity of variance was also found for P. albicaulis site density on the ridge, north and south plot series

(F-max = 19.8). In addition to descriptive statistics for all plot series, Kruskal-Wallis ANOVA (Siegel 1956) was used to compare results among the three ridge plot series (north, ridge, south). Further comparisons were made with Wilcoxon Rank Sum tests. The non-parametric statistical tests were selected in accordance with Siegel (1956).

The independent sampling, ratio measurement scale, and sample sizes were considered adequate to justify use of parametric analyses for correlation and regression. Pearson Product Moment Correlation analyses (Bailey 1981) were used for testing the following: elevation vs. distance (aerial distance from seed source), distance vs. tree density; distance vs. site density (a site may be one tree or multiple trees in a single cluster); distance vs. tree age; tree height vs. tree age; elevation vs. site density, and elevation vs. tree density for all plot series. North, south and ridge plot series were combined, and scatterplots with simple linear regression lines were calculated for tree density vs. distance, site density vs. distance, $\log_{10}$ of tree density vs. distance, and $\log_{10}$ of site density vs. distance. The $\log_{10}$ of the density was plotted to see if linearity would result. The regression formula was:

$$Y = bX + a$$

where, Y = dependent variable, b = slope, a = y intercept, X = independent variable (Gravetter and Wallnau 1985). The statistical significance of regression coefficient r was determined from Appendix 4 in Bailey (1981). Analyses were run

on an IBM-compatible microcomputer with Microstat (version 4.1, Ecosoft, Inc., Indianapolis, IN).

RESULTS

Plot descriptions

Elevation on the north, south and ridge plots ranged from 2105 m to 2480 m (Table 1). The straight line distance from the eastern edge of individual plots to the seed source ranged from 50 m to 3650 m. The steepest slopes were on the north aspect (range 0 to 50°, mean = 30°), the south was moderately steep (range 0 to 40°, mean 20°), and the ridgetop averaged much flatter (range 0 to 30°, plus one atypical plot with 40° slope, mean = 10°).

For the 14 plots on the road transect, elevation was generally lower than on the ridge series of plots, between 2105 and 2290 m (Table 1). The slope on road plots averaged 20°.

Conifer species and site counts

Four species of conifers were found on each plot series (north, south, ridge, road) (Table 1). Total number of Pinus albicaulis sites was 500. The number of sites of Pinus contorta was higher than that of P. albicaulis on every plot series but the north, despite the smaller P. contorta sampling area. In addition, the

total number of sites of P. contorta (n = 516) was greater than that for each of the other conifers. The following comparison of total sites per species is based on sampling areas of the same size: Pinus contorta > Abies lasiocarpa > Picea engelmannii. Only on the road plot series were A. lasiocarpa site counts (n = 123) higher than counts of P. contorta.

The two unburned forest plots supported predominantly P. albicaulis and A. lasiocarpa, with a few Pinus contorta and Picea engelmannii on the south.

Understory plant species occurrence

A partial sampling of understory plant composition allowed us to make some comparisons among plot series. The major vegetation differences between aspects are the result of differences in occurrence of common species (Fig. 3). The north and south plot series show differences in the relative occurrence of xeric and mesic species, and the ridge was intermediate between north and south. Fig. 3 shows the five most frequently occurring plant species by plot series. These species are dominant species for the Bitterroot region, and are classified as mesic or meso-xeric (Lackschewitz 1986). Grasses and other xeric vegetation were most frequent on the south plot series, and less frequent on the ridge and the north.

Road plots showed some similarities to both the north and ridge plot series. The road plots resembled the north plot series in

rank order of species frequencies on plots, while frequency values for some species on the road plots were similar to the ridge.

The two unburned forest plots exhibited understory occurrences of Xerophyllum tenax, Vaccinium scoparium, and Carex geyeri.

Pinus albicaulis clusters and site vegetation

Cluster sizes (number of individual trees per Pinus albicaulis site) ranged overall from 1 to 9 (Table 2). The ridge and north plot series showed a range of 1 to 8, the south 1 to 5, and the road 1 to 9. In all tests, results were considered significant only if $P < .05$. Kruskal-Wallis ANOVA indicated a significant difference in cluster size among the three ridge plot series ($H = 6.475$, $df = 2$, $P = 0.039$). Further analysis with the Wilcoxon Rank Sum test showed cluster sizes on south plots differing significantly both from the north ($Z = 1.951$, $P = 0.026$) and the ridge ($Z = -2.543$, $P = .006$).

On every plot series, the largest percentage of sites were solitary trees (south - 66.2%, north - 52%, road - 51.1%, ridge - 45.4%). As cluster size increased, the percentage of clusters in each size category decreased. One exception was on the road plot series, where clusters of 3 trees accounted for 22.2% of all sites, and clusters of 2 trees accounted for only 6.7%. A cluster containing 17 trees was found near a road plot; this is larger than the cluster size range of 1 to 15 previously reported

by Tomback (1982).

Pinus albicaulis sites on the three different ridge plot series showed dissimilar frequency percentages of site vegetation species, but similar rank order of frequency. Vaccinium scoparium was most frequent on all plot series, and Polytrichum sp. or Carex rossii was the second most frequent. Many P. albicaulis trees were growing in the middle of a clump of C. rossii. On north and ridge sites, V. scoparium frequency was 86% and 69.7%, respectively; and all other species accounted for 25% or fewer occurrences. South plot series P. albicaulis sites showed no site plant species frequency greater than 25% (Fig. 4). Despite the frequent occurrence of Xerophyllum tenax on many plots, no P. albicaulis trees were actually growing within these formidable clumps.

Nearest objects

Five categories of objects were noted on Pinus albicaulis sites within 15 cm of the tree trunk(s). Wood pieces were the nearest object on 122 sites (24.4%), a log or single large branch on 112 (22.4%), a fallen snag on 69 (13.8%), rocks on 68 (13.6%), and a standing snag or stump on 34 (6.8%). Ninety-five (19%) of the sites were categorized as 'open', because no object was present.

Vegetation comparisons between plot series and *Pinus albicaulis* sites

Analysis of vegetation on *P. albicaulis* sites shows both similarities and differences compared to the vegetation frequencies on plot series. *Vaccinium scoparium* was the most frequently occurring species on tree sites on all plot series, with a frequency on ridge sites intermediate between north and south, and a frequency on the road sites most resembling that of the ridge. *Vaccinium scoparium* showed the same frequency pattern on plots as it did on tree sites for the three ridge plot series. *Polytrichum*, a mesic species, was the second most frequently occurring species on north and road sites and also showed high occurrences on north and road plots.

Distinct differences between site vegetation and plot vegetation are reflected in the frequencies of *Carex rossii* and *Xerophyllum tenax*. Although *C. rossii* is the second most frequently occurring species on ridge and south sites, it ranks much lower in occurrence on ridge and south plots. Conversely, *X. tenax* was present on all south and ridge plots and over 70% of the road and north plots, but occurred on no north sites and on fewer than 8% of sites on the other three plot series.

Conifer densities

A comparison of mean plot densities on the three ridge plot series combined gave the following results: Pinus albicaulis (0.08), Pinus contorta (0.04), Abies lasiocarpa (0.008), and Picea engelmannii (0.003) (Figure 2, Tomback et al. 1989, in press). When individual plot series were analyzed, the mean density rank order changed to P. contorta slightly greater than P. albicaulis on the ridge and the south. Mean plot densities on the road plot series indicated the following ranking, from highest to lowest: A. albicaulis, P. contorta, P. engelmannii, and P. albicaulis.

Pinus albicaulis density, elevation, and distance from seed source

The ranges of Pinus albicaulis site density per m^2 per plot for the ridge, north and south plot series, respectively, were: 0 to 0.192, 0.006 to 0.512, and 0.001 to 0.11 (Table 3). Site densities for the north, ridge and south plot series showed differences of high statistical significance (Kruskal-Wallis ANOVA, $H = 10.614$, $df = 2$, $P < .005$). North plot series site densities differed significantly from the ridge plot densities (Wilcoxon Rank Sum, $Z = 2.758$, $P < .003$) and from the south plot densities ($Z = -3.521$, $P < .001$).

The relationship between P. albicaulis site density (sites per

m^2) and elevation, site density and distance from seed source, and elevation and distance was determined for each plot series (Pearson correlation, Table 4). Elevation and distance from seed source were significantly correlated for all three ridge plot series, but not for the road. Significant negative correlations with $P < .01$ between site density (sites per m^2) and distance from seed source occurred on all series of plots except the road: north, $r = -0.832$; ridge, $r = -0.618$; south, $r = -0.714$ (Table 4). Site density and elevation were significantly correlated for the three ridge plot series with $P < .01$, but not for the road series: north, $r = 0.982$; ridge, $r = 0.632$; south, $r = 0.682$ (Table 4).

A total of 1029 Pinus albicaulis trees (more than one tree may occur at a site) was tabulated on the two study sites: 917 on the ridge (includes ridge, north and south plot series) and 112 on the road plot series (Table 3). Mean tree densities per m^2 were: north - 0.275, ridge - 0.099, south - 0.035, and road 0.051. Kruskal-Wallis ANOVA showed that P. albicaulis tree densities per plot were significantly different among the north, ridge, and south plot series ($H = 14.191$, $df = 2$, $P < .001$). Wilcoxon Rank Sum results were significant for comparisons of the north series vs. both the ridge series ($Z = 2.478$, $P < .007$) and the south series ($Z = 3.616$, $P < .001$). Thus P. albicaulis density is significantly greater on the north than on the other two aspects.

Significant negative correlations ($P < .01$) were found for tree density vs. distance from seed source for all three ridge plot

series (Table 4). Correlations between elevation and tree density were also significant ($P < .01$) for the three ridge plot series (Table 4). Neither correlation was significant for the road plot series.

Regression model for density vs. distance from seed source

Sites.--Data from the north, south and ridge plot series were combined in a scatterplot of Pinus albicaulis site density (dependent variable) vs. distance from seed source (independent variable). The plot produced a negative exponential curve with the following linear regression equation:

$$Y = -0.00006(X) + 0.175$$

($df = 60$, $r = -0.590$, $P < .001$). When $\log_{10}$ density was used, the scatterplot produced a straight line and the regression equation was:

$$Y = -0.0005(X) - 0.806,$$

with $r = -0.692$ and $P < .001$.

Regression analysis of the road plots indicated no correlations between P. albicaulis site density and distance from seed source. Even when the $\log_{10}$ density was used, the regression was not significant.

Trees.--Combining north, ridge and south plot series, the scatterplot for tree density against distance also assumed a negative exponential curve (Fig. 5). The regression equation was:

$$Y = -0.0001(X) + 0.344,$$

with df = 60, r = - 0.571, and P <.001. With $\log_{10}$ of tree density (Fig. 6), the plot became linear and the equation became

$$Y = -0.0005(X) - 0.542$$

with r = -0.666 and P <.001.

The same analysis for P. albicaulis trees on the road plots failed to produce a significant correlation between density and distance.

Tree age and height

Each separate stem within a Pinus albicaulis cluster was considered a tree for aging purposes; the number of trees aged on north plots was 334; on the ridge, 149; and on the south, 79 (Table 3). Field data show that the ages of trees within an individual cluster were the same or similar, any differences were by only 1 or 2 years, but in no case more than 4 years. In virtually all cases no stems were fused at the base, thus it must be emphasized that each member of a cluster appeared to be a distinct individual. The age differences observed were probably the result of later germination or counting error. Age ranges of trees were nearly identical for the three ridge plot series, with the oldest trees at 21 years (Table 3). Forty-seven trees were aged on road plots, with a range of 0.5 to 19 yr and a lower mean (6 yr) than any of the ridge plot series. P. albicaulis trees (n = 63) on the two unburned forest plots showed a mean age of 126

yr and a range of 76 to 202 yr.

Tree heights ranged from 1 to 238 cm. The range and mean for the ridge plot series was the highest, followed by the north, south, and road. Highly significant Pearson correlations ($P < .001$) were found for tree age vs. tree height for all plot series (Table 4).

DISCUSSION

Evaluation of hypotheses

Hypotheses 1 - *Pinus albicaulis* site counts on the three ridge plot series, relative to counts of other regenerating conifers, indicate that it is a major component in the early seral stages of community development. The species is co-dominant with *Pinus contorta* on all aspects, a likely consequence of the abundance of *P. contorta* prior to the fire (Lyon 1976). On the road plot series, however, both *P. contorta* and *Abies lasiocarpa* occur in higher densities than *P. albicaulis*. This may reflect differences in the distance of seed sources for the three conifers, as well as the suitability of sites at lower elevations for *P. albicaulis*. Hypothesis 2 - Regeneration of *P. albicaulis* is underway in the burn, although the oldest trees (21 years) of this slow-growing conifer will not be cone-bearing for another two decades. As predicted, a range of age groups were apparent, from recent germinants to small trees. The oldest tree did not

germinate until 5 years after the burn. This may reflect the interval before a cone crop occurred in the nearby forest. Hypothesis 3 - Results showed a significant negative correlation between P. albicaulis and distance from the seed source for all aspects of the ridge plot series. In fact, the combined scatterplot pattern was a negative exponential curve, indicating an initially rapid decline in density with distance. The relationship between density and distance did not hold for the road plot series. Most of the road plots were at distances much greater from seed source than the ridge plot series. At these distances, the density-distance plot may not change very much. Hypothesis 4 - The patterns of seed dispersal are similar to those observed previously for bird-dispersed pines (Tomback 1982, Tomback 1986). At nearly 50% of the P. albicaulis regeneration sites, seedlings occur in clusters, reflecting an origin in nutcracker caches. In addition, the distances over which seeds were dispersed are typical of nutcracker food-storage activities (Tomback 1978, Vander Wall and Balda 1977). There is no other mechanism that would enable a heavy, wingless seed to be dispersed as far as 8 km.

Regeneration: consequences of seed dispersal by Nutcrackers

Regeneration patterns of Pinus albicaulis in the Sleeping Child Burn demonstrate the importance of nutcrackers as seed

dispersers. A few nutcrackers were seen in the study site during field work in 1987, but the lack of a P. albicaulis cone crop that year prevented direct observation of foraging or caching behavior. However, the occurrence of tree clusters and the great distances from regeneration to seed source confirm previous suggestions that nutcrackers are the primary dispersers of P. albicaulis and that their caching behaviors effect establishment of the conifer (Lanner 1980; Hutchins and Lanner 1982; Tomback 1982). This study also confirms that squirrels and other rodents play a very minor role at best in the dissemination of Pinus albicaulis. As reported by Hutchins and Lanner (1982), red squirrels (Tamiasciurus hudsonicus), chipmunks and other mammals are not reliable dispersers compared to nutcrackers. Their limited home ranges indicate that a more mobile disperser has buried seeds to account for the observed distances between seed source and regeneration. Although Stellar's jays (Cyanocitta stelleri) were seen in the study area, they also establish small territories, damage seeds upon removal from the cone, and bury one-seed caches (Vander Wall and Balda 1977). Nearly half of all Pinus albicaulis sites were composed of two or more trees, with clusters of up to 9 trees observed on the road plot series, and a cluster of 17 trees observed near that transect. The distinct multiple stems and the similarity in tree ages within a cluster are evidence of germination from buried seed caches.

Interestingly, no P. albicaulis older than 21 yr was found on the plots, even though the burn occurred 26 years prior. This

may indicate a lack of regeneration during the five years immediately following the burn, either because of unfavorable conditions for seed germination or no cone crops.

Dispersal distances of P. albicaulis in the Sleeping Child Burn are similar to the distances noted by Tomback (1978) and Hutchins and Lanner (1982), although their studies occurred in California and Wyoming, respectively. Regeneration from the seed source in the adjacent forest extended into the burn westward for 3.65 km and southward nearly 8 km. Because P. albicaulis trees were found on the study plots furthest from the seed source, we assume regeneration has occurred beyond these distances also. These spatial patterns lead us to conclude that nutcrackers are responsible for the observed P. albicaulis regeneration in the burn.

An interesting pattern with potential application was the significant linear relationship observed between the density of regenerating P. albicaulis on the three ridge plot series and the aerial distance from the seed source (Figures 5 and 6). This correlation reflects the dispersal pattern generated by the nutcracker. Elevation also correlated significantly with distance from seed source on the three ridge plot series (Table 4), but at this time it is not possible statistically to separate the effect of elevation on density from the effect of distance on density. Long lived caches of P. albicaulis are common in Pinus ponderosa forests as low as 1160 m elevation in western Montana, thus there is little reason to suspect that the relatively modest

elevational range of the ridge transect (on an open burned site) would greatly affect survival of P. albicaulis (Arno and Hammerly 1984). However, P. albicaulis grows well in western Montana from elevations of 2290 - 2620, and nearly half of the plots on each series were within the 2290 - 2620 m range (Fig. 6). Thus, the pattern generated should primarily reflect differences in distance and not elevation effects.

The regeneration patterns that result from nutcracker seed dispersal along a distance gradient from a known seed source suggest that the birds cache relatively more seeds close to the parent trees and make fewer caches per m^2 at increasing distances. The result is a negative exponential curve (tree density vs. distance) (Fig. 6), a shape similar to the seed shadow curves generated by individual wind-dispersed conifers (McCaughey et al. 1986), but with the P. albicaulis regeneration extended over much greater distances. As discussed by Tomback et al. 1989, submitted), the dispersal distances for P. albicaulis appear to typically be greater than that for Abies lasiocarpa, which replaces P. albicaulis as succession advances. This nutcracker-mediated dispersal gives P. albicaulis a necessary advantage over Abies lasiocarpa.

The negative exponential curve was confirmed as well for P. albicaulis regeneration in the Saddle Mountain Burn to the south of the Sleeping Child Burn (Tomback et al. 1989, in press, Tomback et al. 1989, submitted). For management purposes, this curve may be useful for its predictive value (e.g., Keane et al.,

in press). Potential application includes models of P. albicaulis regeneration for prescribed fires or for past fires, such as in high elevation areas of Yellowstone National Park burned in 1988.

The correlation between density and distance did not hold for the road plot series. The reason for this road transect pattern is unknown, but the data is weaker than for the ridge transect or the Saddle Mountain transects. All of the road series plots were at elevations of 2290 m or less, and thus were below the range within which P. albicaulis grows well in this region.

Variation in density and cluster size

The data show significantly higher densities of both Pinus albicaulis sites and trees on the north aspect of the ridge than on the ridge or south (at least 7 times greater mean density on the north). This is consistent with the prevalence of P. albicaulis on cool exposures and moist sites in semiarid ranges (Arno and Hoff 1989). North slopes, with deeper soil mantles, more moisture and cooler temperatures, may provide more suitable germination conditions. Leadem (1986) examined the dormancy-breaking mechanisms of P. albicaulis seeds, and found that cold temperatures were necessary to overcome physiological barriers to growth. Alternatively, nutcrackers may cache more on north slopes, but Tomback (1978, 1982) and Vander Wall and Balda (1977) suggest that south slopes are preferred. Snow on steep south

exposures melts off early in the spring, coinciding with a time when nutcrackers are seeking food for their nestlings (Tomback 1978). Thus cache recovery may be concentrated on south slopes. North slopes do not melt off until later, when nutcrackers may have migrated to higher elevations. Regeneration density must be a result of: 1) nutcracker caching preferences, 2) nutcracker cache recovery success, and 3) site quality. Competition from other plant species could also be a factor in density variation among plot series. Xerophyllum tenax tufts were widespread on south slopes, as were grass species; both are potential competitors for young trees.

Anotner interesting pattern was the relatively large cluster sizes found on the road plot series, where the largest percentages of cluster sizes greater than 5 occurred, and a 17-stem cluster was found nearby. Distances from road plots to the seed source averaged over twice as far as ridge plots. This poses an interesting question: do nutcrackers bury larger clusters of seeds when they fly greater distances? Although highly tolerant of crowding, P. albicaulis seedlings within a cluster compete as they mature. The lower height values observed for trees on the road plot series could be indicative of greater competition within larger clusters.

Post-fire disturbance

Successional processes have been complicated by a history of

1986).

Fire and P. albicaulis regeneration

Twenty-six years after a severe fire, the Sleeping Child Burn shows regeneration of Pinus albicaulis to be well under way. Tree counts of the four conifer species on the higher elevation study site (the three ridge plot series) support the observation that stand-replacing fires favor P. albicaulis in relation to its more shade-tolerant subalpine associates, Abies lasiocarpa and Picea engelmannii (Arno 1986, Arno and Hoff1989). This pattern is complicated by a higher density of Pinus contorta on the plots with south exposures and on the few plots at the west end of the ridge that are within lower subalpine elevations. The striking abundance of P. contorta regeneration on the lower subalpine road plots is due to the seral P. contorta forest existing at the time of the fire. Large numbers of seeds were released as the serotinous cones opened from the heat (Fischer and Bradley 1987). Our two plots in the unburned forest at the upper edge of the burn show species composition dominated by P. albicaulis and by A. lasiocarpa, a species that usually replace P. albicaulis in most subalpine areas (Pfister et al. 1977).

Tree counts for the road plot series show Pinus albicaulis regeneration to be a relatively minor component in relation to Abies lasiocarpa and Pinus contorta.

Clearly, the result of severe fire in the Sleeping Child Burn

disturbances in the study area. Lyon (1976) summarized several years of post-fire management activities in the Sleeping Child burn, including chemical thinning of lodgepole pine, pole cutting, cattle grazing, Christmas tree cutting, firewood gathering, road building, aerial sowing of annual grasses, and recreational uses such as hunting and camping. He estimates little long-term effect from these management activities, since competition would have produced substantial losses in dense stands anyhow. However, some of these activities, especially chemical thinning of Pinus contorta, grazing, and sowing of grasses, may affect the type and density of regrowth within some areas of the burn. A case in point is the road plot series, with an elevation range stated to be dominated by P. contorta prior to the fire (Lyon and Stickney 1976), but with regeneration density of P. contorta lower than Abies lasiocarpa. Range cattle were encountered during field work, and evidence of grazing and browsing was seen often on gentle slopes in both study sites.

Vegetation comparisons between plots and sites

Overall, much consistency was seen in the understory species at Pinus albicaulis sites, despite differences in characteristic vegetation found on the four plot series. The predominance of species such as Vaccinium scoparium, Polytrichum sp., and Carex rossii at tree sites reflects the preference of P. albicaulis for mesic to meso-xeric habitat in these mountains (Lackschewitz

is regeneration of P. albicaulis at higher elevations. The post-fire dominance of this species is apparently typical of the forest overstory composition for much of the northern Rocky Mountains that existed prior to 20th century fire suppression policies.

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LITERATURE CITED

------. 1986. Whitebark pine cone crops - a diminishing source of wildlife food? Western Journal of Applied Forestry 1: 92-94.

Arno, S. F., and T. D. Petersen. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Forest Service Research Paper INT-301. United States Department of Agriculture, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Arno, S. F., and R. P. Hammerly. 1984. Timberline: Mountain and Arctic Forest Frontiers. Seattle, WA. The Mountaineers. 304 p.

Arno, S. F., D. G. Simmerman, and R. E. Keane. 1985. Forest succession on four habitat types in western Montana. Forest Service General Technical Report INT-177. United States Department of Agriculture, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Arno, S. F., and R. J. Hoff. 1989. Silvics of Whitebark Pine (Pinus albicaulis). GeneralTechnical Report INT-253. United States Department of Agriculture, Intermountain Research Station, Ogden, Utah, USA.

Arno, S. F., and T. Weaver. 1989. Whitebark pine community types

and their patterns on the landscape. Symposium proceedings, Wyman Schmidt (compiler): Whitebark Pine Ecosystems - Ecology and Management of a High Mountain Resource, Bozeman, Montana. USDA Forest Service General Technical Report, INT-.

Bailey, N. T. J. 1981. Statistical Methods in Biology, Second Edition. John Wiley and Sons, New York, New York, USA.

Dorn, R. D. 1984. Vascular Plants of Montana. Mountain West Publishing, Cheyenne, Wyoming, USA.

Finklin, A. I. 1983. Weather and Climate of the Selway-Bitterroot Wilderness. University Press of Idaho, Boise, Idaho, USA.

Fischer, W. C., and A. F. Bradley. 1987. Fire ecology of western Montana forest habitat types. Forest Service General Technical Report INT-223. United States Department of Agriculture, Intermountain Research Station, Ogden, Utah, USA.

Furnier, G. R., P. Knowles, M. A. Clyde, and B. P. Dancik. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution 41: 607-612.

Gravetter, F. J., and L. B. Wallnau. 1985. Statistics for the Behavioral Sciences. West Publishing Company, St. Paul,

Minnesota, USA.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington, USA.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia (Berl)(1982) 55: 192-201.

Keane, R. E., S. F. Arno, J. K. Brown, and D. F. Tomback. In press. Modeling stand dynamics in whitebark pine forests. Ecological Modelling.

Kendall, K. C. 1980a. Bear-squirrel-pine nut interaction, 1978-79. Pages 51-60 in Yellowstone grizzly bear investigations. Annual Report 1978-79, United States Department of the Interior, National Park Service.

Kendall, K. C. 1980b. Food habits of Yellowstone grizzly bears, 1978-79. Pages 24-34 in Yellowstone grizzly bear investigations. Annual Report 1978-79, United States Department of the Interior, National Park Service.

Kendall, K. C., and S. F. Arno. 1989. Whitebark pine: and important but endangered food for wildlife. Symposium

proceedings, Wyman Schmidt (compiler): Whitebark Pine Ecosystems - Ecology and Management of a High Mountain Resource, Bozeman, Montana. USDA Forest Service General Technical Report INT-.

Lackschewitz, K. 1986. Plants of west-central Montana - Identification and ecology: annotated checklist. Forest Service General Technical Report INT-217. United States Department of Agriculture, Intermountain Research Station, Ogden, Utah, USA.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Pages 14-48 in B.P. Dancik and K.O. Higginbotham, editors. Proceedings of the Sixth North American Forest Biology Workshop. University of Alberta, Edmonton, Alberta, Canada.

Leadem, C. L. 1986. Seed dormancy in three Pinus species of the inland mountain west. Pages 117-124 in R. C. Shearer, editor. Proceedings - Conifer Tree Seed in the Inland Mountain West Symposium. Forest Service General Technical Report INT-203. United States Department of Agriculture, Intermountain Research Station, Ogden, Utah, USA.

Linhart, Y. B., and D. F. Tomback. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia (Berlin) 67: 107-110.

Lotan, J. E. 1975. The role of cone serotiny in lodgepole pine forests. In Management of Lodgepole Pine Ecosystems Symposium Proceedings. Washington State University Cooperative Extension Service, Pullman, Washington, USA.

------. 1976. Cone Serotiny - Fire relationships in lodgepole pine. In Proceedings, Tall Timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council Fire and Land Management Symposium. Tall Timbers Research Station, Tallanassee, Florida, USA.

Lyon, L. J. 1976. Vegetal development on the Sleeping Child burn in western Montana 1961 to 1973. USDA Forest Service Research Paper INT-184. Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Lyon, L. J., and P. F. Stickney. 1976. Early vegetal succession following large Northern Rocky Mountain wildfires. Pages 355-375 in Proceedings, Montana Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium, No. 14, 1974: 355-375. Tall Timbers Research Station, Tallahassee, Florida, USA.

McCaugney, W. W., W. C. Schmidt, and R. C. Shearer. 1986. Seed-dispersal characteristics of conifers in the inland mountainous west. Pages 50-62 in R. C. Shearer, editor, Proceedings - Conifer Tree Seed in the Inland Mountain West Symposium. Forest Service

General Technical Report INT-203. United States Department of Agriculture, Intermountain Research Station, Ogden, Utah, USA.

Mirov, N. T. 1967. The Genus Pinus. Ronald Press Company, New York, New York, USA.

Mirov, N. T., and J. Hasbrouck. 1976. The Story of Pines. Indiana University Press, Bloomington, Indiana, USA.

Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. Forest Service General Technical Report INT-34. United States Department of Agriculture, Intermountain Forest and Range Experiment Station, Ogden, Utan, USA.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52: 199-221.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York, New York, USA.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. The Living Bird (16th Annual, 1977): 123-161.

------. 1982. Dispersal of whitebark pine seeds by Clark's

nutcracker: a mutualism hypothesis. Journal of Animal Ecology 51: 451-467.

------. 1983. Nutcrackers and pines: coevolution or coadaptation? Pages 179-223 in M.H. Nitecki, editor. Coevolution. University of Chicago Press, Chicago, Illinois, USA.

------. 1986. Post-fire regeneration of krummholz whitebark pine: consequence of nutcracker seed caching. Madrona 33: 100-110.

Tomback, D. F., L. A. Hoffmann, and S. K. Sund. 1989. In press. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: W. Schmidt, compiler, Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High Mountain Resource. Bozeman, MT, USA.

Tomback, D. F., S. K. Sund, and L. A. Hoffmann. 1989. Comparison of whitebark regeneration patterns on two burn. Aubmitted, Ecology

USDA Soil Conservation Service. 1977. Average annual precipitation, Montana, based on 1941-1970 period. USDA-SCS, Bozeman, Montana, USA.

Vander Wall, S. B., and R. P. Balda. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs 47: 89-111.

Wright, H. A., and A. W. Bailey. 1982. Fire Ecology: United States and Southern Canada. John Wiley and Sons, New York, USA.

APPENDIX 1

TABLE A1. Plant species encountered during this study in the Sleeping Child Burn. Compiled from Dorn (1984) and Hitchcock and Cronquist (1973).

	COMMON NAME	SCIENTIFIC NAME
1	Subalpine fir	*Abies lasiocarpa*
2	Yarrow	*Achilles millefolium* v. *alpicola*
3	Pearly-everlasting	*Anaphalis margaritacea*
4	Pussytoes	*Antennaria* sp.
5	Sandwort	*Arenaria aculeata*
6	Arnica	*Arnica cordifolia*
7	Mountain arnica	*Arnica latifolia* v. *latifolia*
8	Aster	Family *Asteraceae*
9	Smooth brome-grass	*Bromus inermis* ssp. *inermis*
10	Elk sedge	*Carex geyeri*
11	Ross sedge	*Carex rossii*
12	Composite (unknown)	Unknown composite
13	Orchard-grass	*Dactylis glomerata*
14	Fireweed	*Epilobium* sp.
15	Buckwheat	*Eriogonum* sp.
16	Fleabane	*Erigeron* sp.
17	Forb (unknown)	Unknown forb

18	White hawkweed	*Hierachium albiflorum*
19	Western hawkweed	*Hierachium albertinum*
20	Labrador tea	*Ledum glandulosum*
21	Patridge foot	*Leutkea pectinata*
22	Lichen (unknown)	Unknown lichen
23	Honeysuckle	*Lonicera utahensis*
24	Lupine	*Lupinus* sp.
25	Woodrush	*Luzula* sp.
26	Fools huckleberry	*Mensiesia ferruginea* v. *glabella*
27	Alpine fernleaf	*Pedicularis contorta*
28	Penstemon	*Penstemon procerus*
29	Common timothy	*Phleum pratense*
30	Engelmann spruce	*Picea engelmannii*
31	Whitebark pine	*Pinus albicaulis*
32	Lodgepole pine	*Pinus contorta* v. *latifolia*
33	Ponderosa pine	*Pinus ponderosa* v. *scopulorum*
34	Bluegrass	*Poa* sp.
35	Bistort	*Polygonum bistortoides*
36	Moss	*Polytrichum* sp.
37	Jacobs ladder	*Polemonium* sp.
38	Douglas-fir	*Pseudotsuga menziesii*
39	Gooseberry	*Ribes* sp.
40	Sheepsorrel	*Rumex acetosella*
41	Catchfly	*Silene spaldingi*
42	Green needlegrass	*Stipa nelsonii*
43	Needlegrass	*Stipa occidentalis*

44	Snowberry	*Symphoricorpus* sp.
45	Dandelion	*Taraxacum officinales*
46	Downy oatgrass	*Trisetum spicatum*
47	Huckleberry	*Vaccinium globulare*
48	Grouseberry	*Vaccinium scoparium*
49	False hellebore	*Veratrum viride*
50	Beargrass	*Xerophyllum tenax*

TABLE 1. Plot series characteristics: aspect (deg), elevation (m), distance from *P. albicaulis* seed source, slope (deg), area per plot (m^2), number of sites, total sampling area (m^2).

TABLE 2. *Pinus albicaulis* clusters: size and frequency.

TABLE 3. *Pinus albicaulis* regeneration by plot series: density per plot (sites or trees/m^2), age (yrs), height (cm). N = total number.

TABLE 4. Pearson correlation analysis: elevation vs. distance from seed source, *Pinus albicaulis* density (sites or trees per m^2) vs. elevation, density vs. distance, age vs. height. (NS = not significant, $P>.05$). Log = Log_{10}. In all cases, df = no. of plots minus two.

FIG. 1. Study site #1: Sleeping Child Burn, Ridge Transect. The stippled area is the subalpine forest bordering the burn. The hatchmarked area indicates a subsection of the forest with elevations above 2257 m where continuous stands of *P. albicaulis* provide the seed source for regeneration.

FIG. 2. Study site #2: Sleeping Child Burn, Road Transect. The stippled area is the subalpine forest bordering the burn. The hatchmarked area indicates a subsection of the forest with elevations above 2257 m where continuous stands of *P. albicaulis*

provide the seed source for regeneration.

FIG. 3. Five most frequently occurring plant species on plots, by plot series.

FIG. 4. Five most frequently occurring plant species on *P. albicaulis* sites, by plot series.

FIG. 5. Scatterplot of *P. albicaulis* tree density vs. distance, for three ridge plot series combined.

FIG. 6. Scatterplot of *P. albicaulis* $\log_{10}$ tree density vs. distance and elevation, for three ridge plot series combined.

TABLE 1. Plot series characteristics

	PLOT SERIES			
	NORTH	RIDGE	SOUTH	ROAD
Total number of plots	21	23	19	14
General aspect	north	west	south	north
Aspect range (deg)	290-20	90-330	170-230	330-90
Mean elevation (m)	2305	2305	2295	2200
Elevation range (m)	2150-2475	2175-2480	2165-2465	2105-2290
Distance from *P. albicaulis* seed source (m)	50-3500	50-3650	50-3450	900-7950
Mean slope (deg)	30	10	20	20
Slope range (m)	0-50	0-40	0-40	0-30
Area per plot (m^2):				
Mean	154.8	201.1	228.9	84
Range	62.5-500	62.5-500	62.5-750	12.5-500
Number of sites:				
P. albicaulis	271	119	65	45
P. contorta	115	186	135	80
A. lasiocarpa	33	21	6	123
P. engelmannii	19	16	2	36
Total sampling area (m^2):				
P. albicaulis	3500	5750	6225	2975
Other*	3250	4625	4350	1176

* *P. contorta*, *A. lasiocarpa*, and *P. engelmannii* combined.

TABLE 2. Number of seedlings per *Pinus albicaulis* regeneration site

	PLOT SERIES			
	NORTH	RIDGE	SOUTH	ROAD
Number of sites	271	119	65	45
Number of trees per site:				
Mean	1.92	2.06	1.57	2.49
Range	1-8	1-8	1-5	1-9
Cluster size	Frequencies (%)			
1	52.0	45.4	66.2	51.1
2	26.6	28.6	21.5	6.7
3	8.5	12.6	4.6	22.2
4	6.3	6.7	4.6	6.1
5	4.8	4.2	3.1	2.2
6	1.1	0.8	--	4.4
7	0.4	0.8	--	2.2
8	0.4	0.8	--	2.2
9	--	--	--	2.2

TABLE 3. *Pinus albicaulis* regeneration by plot series

	PLOT SERIES			
	NORTH	RIDGE	SOUTH	ROAD
Sites				
Total number	271	119	65	45
Range per plot	1-32	0-24	1-11	0-10
Density per plot (sites/m^2):				
Mean	0.14	0.04	0.02	0.02
Range	0.006-0.512	0-0.192	0.001-0.11	0-0.007
Trees				
Total number	520	245	102	112
Range per plot	1-61	0-56	1-13	0-22
Density per plot (trees/m^2):				
Mean	0.275	0.099	0.035	0.051
Range	0.006-0.976	0-0.448	0.001-0.13	0-0.127
Tree Age (yr)				
Total number	334	149	79	47
Mean	7.7	8.3	8.1	6
Range	1-21	0.5-20	1-21	0.5-19
Tree Height (cm)				
Mean	29.7	36.2	30.6	19.2
Range	1.5-234	3-238	3-202.3	1-186

Table 4. Pearson correlation analysis for P. albicaulis

	PLOT SERIES	NO. OF PLOTS	CORRELATION COEFFICIENT(r)	P
Elevation vs. distance	North	21	0.958	<.01
	Ridge	23	0.961	<.01
	South	19	0.961	<.01
	Road	14	0.574	NS
Site density vs. elevation	North	21	0.982	<.001
	Ridge	22	0.632	<.01
	South	19	0.682	<.01
	Road	13	0.429	NS
Tree density vs. elevation	North	21	0.877	<.001
	Ridge	22	0.647	<.01
	South	19	0.662	<.01
	Road	13	0.194	NS
Site density vs. distance	North	21	-0.832	<.001
	Ridge	22	-0.618	<.01
	South	19	-0.714	<.001
	Road	13	-0.374	NS

TABLE 4. Continued.

	PLOT SERIES	NO. OF PLOTS	CORRELATION COEFFICIENT(r)	P
Log site density vs. dist.	North	21	-0.820	<.001
	Ridge	22	-0.733	<.001
	South	19	-0.779	<.001
	Road	13	-0.500	NS
Tree density vs. distance	North	21	-0.822	<.001
	Ridge	22	-0.627	<.01
	South	19	-0.703	<.001
	Road	13	-0.207	NS
Log tree density vs. dist.	North	21	-0.788	<.001
	Ridge	22	-0.751	<.001
	South	19	-0.678	<.01
	Road	13	-0.334	NS
Tree age vs. height	North	334	0.818	<.001
	Ridge	149	0.753	<.001
	South	79	0.827	<.001
	Road	47	0.742	<.001